SOCIAL AND THERMOREGULATORY BEHAVIOUR OF THE NEW ZEALAND FUR SEAL, *ARCTOCEPHALUS FORSTERI* (LESSON, 1828).

A Thesis presented for the degree
Master of Science
in
Zoology,
University of Canterbury,
Christchurch, New Zealand.

by
Edward H. Miller

November 1971

"... naturalists especially, ought to drape a tunic of gauze around the loins of truth, and to do it with some regard to elegance of appearance."

Henri Fabre.

List of important corrections to: Miller, E. H. 1971. Social and thermoregulatory behaviour of the New Zealand fur seal, Arctocephalus forsteri (Lesson, 1828). Unpublished MSc thesis, Department of Zoology, University of Canterbury, Christchurch, New Zealand.

p. 30: line 5 read "Figure 10"

p. 99: line 24 delete "16 C, D"

p. 100: par. 2, line 20 read "17" for "26"

p. 102: line 10 read "Plates 15C, 20B"

p. 104 last line read "the male has his mouth almost closed, and tension of the expressive muscles is maximal."

p. 105: line 9 read "14A, B, 23A, C"

p. 105: line 10 delete "five"

p. 106: fifth last line read "territorial male"

p. 109: last line read "certain" for "different"

p. 120: second last line read "Plate 24" for "Plate 23"

p. 130: seventh last line read "$H' = -\sum p_i \log p_i$"

p. 137: line 2 read "Figure 47" for "Figure 55"

p. 145: line 9 read "There are no discernible..."

p. 145: fourth last line read "Figures 52, 53" for "Figure 53"

p. 145: second last line read "overall seasonal decline"

p. 189: par. 2, lines 7-11, replace"Also shown are...into total births." by "The 'average harem size' of Kenyon et al.(1954: 51) for the main and subsidiary study areas was 6.8 and 3.8, respectively."

p. 189: par. 2, line 11 read "For the present calculation of 'average harem size', I have..."

p. 190: second last line read "5.8" for "17.6"

p. 202: seventh and eighth last lines read "Plates 37 C and D"

p. 237: seventh last line read "17 to 19" for "17 to 10"

Figure 32A: read "a = oriented away"

Figure 37: add "The vertical arrows indicate one less male-pair for the remainder of the curve."

Figure 38: add "The diagonal line in B indicates that no sample was available for that age combination."

Figure 43: add: "A: data from Table 29; B: data from Table 30. a = run approach/walk approach; lw = lunge/swing; ls = lunge-sprawl; c = dontact.

Figure 51: add "Means ± 95% C.L."

Figure 58: second sentence read "The horizontal lines represent the figures for 'actual mean sex ratios', as defined in the text."

Figure 59B: read "birth" for "copulation"
add "Means are given as births per hour."
For day, replace $\bar{Y} = 4.4$ by $\bar{Y} = 4.2$; for night replace $\bar{Y} = 4.5$ by $\bar{Y} = 5.1$.

Table 26: is missing from at least two copies. If your volume has Table 26, I would appreciate receiving a photocopy of it.

Table 48: column headings, left to right, should read "Vocalization, Distance, Contexts, Characteristics"

Table 54A: read "$0.05 < P < 0.1$ n.s."
54B read "$0.01 < P < 0.025$"

Table 66: column "TOTAL TIME" read "11±0.5" for "11+0.5", "8.6+" for "8.6", and "14.2+" for "14.2"

Chapter IV: the regression equations for Table 83 are incorrect. The discussion based on those equations is qualitatively correct, however, and one regression was significant that is not included in Table 83: "V wet".

If you uncover other important errors, I would be happy to know of them.

Edward H. Miller,
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CHAPTER I. INTRODUCTORY.

A. Introduction.

Since 1871, when Darwin's first edition of The Descent of Man and Selection in Relation to Sex was published, there have appeared numerous studies of sexual dimorphism and sexual selection in fossil and extant taxa. Principles elucidated by Darwin on the choice of, and competition for mates, have since been supported by additional evidence, but is has become apparent that the causes and functions of sexual dimorphism are more diverse than Darwin envisaged (Huxley, 1938a, b).

Published studies on sexual dimorphism in birds, fish, and arthropods are numerous, but there are remarkably few on mammals. The functioning of sexual selection is implicit, however, in the interpretation of such researches as those of Bannikov (1958) on the saiga antelope, Saiga tatarica, by Geist (1966a, b) on artiodactyls, and by Hall (1964) on primates.

The objective of the present study was to examine the social behaviour of the New Zealand fur seal, Arctocephalus forsteri (Lesson), with emphasis on the role played by sexual dimorphism, and the relationship of social structure to thermoregulatory requirements and topography. This species, like all otariids, is polygynous and sexually dimorphic. It breeds in discrete, established colonies, is ashore in large numbers during the breeding season, and is readily observed. Territorial males fast while ashore, and normally do not leave their stations until defeated by challenging males or until the end of the breeding season. Their social contacts during the reproductive period can therefore be readily monitored. Individually recognizable animals are a requisite for successful field behaviour studies, and it was known from work on Zalophus

(Peterson and Bartholomew, 1967), Callorhinus (Bartholomew and Hoel, 1953; Bartholomew, 1953; Kenyon, 1960; Peterson, 1965, 1968), Eumetopias (Gentry, 1970; Sandegren, 1970), A. p. pusillus (R. W. Rand, 1967) and A. townsendi (Peterson and Ramsey, 1968; Peterson et al. 1968), that many animals can be individually recognized by natural scars and marks, or can be approached and marked by paint, dye, or hair-clipping (see Appendix A for nomenclature used in this text). Although numerous publications have appeared on the general biology and behaviour of the genus Arctocephalus, none has approached the degree of refinement of studies on the reproductive and social behaviour of the two northern otariids Callorhinus (Peterson, 1965) and Eumetopias (Gentry, 1970; Sandegren, 1970).

B. Literature review: General

Literature on the behaviour of pinnipeds is voluminous, and only major references are listed below.

Social behaviour and the annual cycle of the highly polygynous southern elephant seal have been treated by Laws (1956), Carrick, Csordas and Ingham (1962), and Carrick et al. (1962). The social system of its northern congener has been studied by Bartholomew (1952), LeBoeuf and Peterson (1969a), and LeBoeuf (1971). Social structure in the only other truly land-breeding, polygynous phocid, Halichoerus, has been discussed by Hewer (1957, 1960), Hewer and Backhouse (1960), Coulson and Hickling (1964), Darling and Boyd (1969), Backhouse (1969) and Cameron (1967, 1971).

Northern sea lions (Zalophus and Eumetopias) have been studied intensively in recent years. Major recent works on the behaviour of Eumetopias are Orr and Poulter (1967), Sandegren (1970), and Gentry (1970). General

and reproductive behaviour of Zalophus was studied by Eibl-Eibesfeldt (1955) and Peterson and Bartholomew (1967). The South American sea lion is the best-known of the southern hemisphere sea lions, and its social behaviour was reported on by J. E. Hamilton (1934). The behaviour of Neophoca and Phocarctos is almost unknown, but a brief account of social behaviour in the former species was given by Marlow (1968).

Callorhinus ursinus, the northern fur seal, has been the subject of some excellent behavioural studies. Bartholomew (1953) and Bartholomew and Hoel (1953) discussed social structure and reproductive behaviour. These reports were followed by studies on female-pup relations (Bartholomew, 1959), and territoriality (Kenyon, 1960; Bychkov and Dorofeev, 1962). Peterson described pup behaviour (1961), and general reproductive behaviour (1965, 1968). A study on interspecific relationships was made by Belkin (1966).

All fur seals of the predominantly southern genus Arctocephalus have been studied to some extent, and reports on their general behaviour are available. Vaz Ferreira has contributed most to our knowledge of A. australis, but translations of his work are not readily available. A. p. pusillus has been extensively studied by R. W. Rand (1955, 1956a, 1959, 1967). The general habits of the South Australian fur seal, A. p. doriferus, have been discussed by Warneke (1966). Good accounts of the general biology and behaviour of the Antarctic fur seals (A. tropicalis and A. gazella) are available. Bonner pioneered work on the general behaviour of A. gazella (Bonner, 1958, 1968; Bonner and Laws, 1964), while Paulian (1964) studied the more northerly A. tropicalis. The rare Guadalupe fur seal (A. townsendi) of the northern hemisphere has been

afforded general treatment by Peterson and Ramsey (1968), and Peterson et al. (1968).

C. Literature review: *Arctocephalus forsteri*.

Most of the early literature on *A. forsteri* in New Zealand and Australia was concerned with physical descriptions, alpha taxonomy (e.g. Hector, 1871; Webb, 1871; Clark, 1875; Forbes, 1892; Scott and Lord, 1925a,b; Jones, 1925a,b), the history of exploitation and natural history (e.g. Clark, 1873; F. R. Chapman, 1893; Allen, 1899; Hutton and Drummond, 1904; McNab, 1907; E. A. Wilson, 1907; Waite, 1909; Thomson, 1921; LeSoeuf, 1925). A short note by Hector (1892: 258) is one of the few reports based on original field observations in that period. More recent publications have been based on field observations, but the sparse information is widely scattered in reports of restricted circulation (e.g. Richdale n.d.; Cox, Taylor and Mason, 1967) and in popular articles and books on natural history (e.g. E. C. Richards, 1952; Gillham, 1967). There are miscellaneous accounts available on helminth parasites (Johnston and Mawson 1953), lack of blood parasites (Laird, 1951: 11-12), skin glands (Ling, 1965), moulting (Ling, 1970), the annual cycle (Ling, 1969), food (Street, 1964), diurnal rhythms (Stirling, 1968), the history of management in New Zealand (Sorensen, 1969a), sexual dimorphism in pups (Crawley and Brown, in press), and fossils (summary given by Fleming, 1968). Two undergraduate projects were carried out on general behaviour (D. L. Brown, 1969; Wood, 1970), and general observations on behaviour were published by Stirling (1970).

The present taxonomic status of the fur seals of Australia and New Zealand has been largely clarified by King (1968, 1969), Shaughnessy (1970), and Stirling and

Warneke (1971). Their researches indicate that the fur seal on the southern central and south western coastline of Australia is conspecific with that found in New Zealand waters, but distinct from the form inhabiting southeastern Australia (A. p. doriferus). Shaughnessy's data also indicate a genetic difference between Australian and New Zealand A. forsteri. In this thesis, the name A. forsteri will be modified by 'New Zealand' or 'Australian' where the context is ambiguous.

D. Arctocephalus forsteri: description.

For descriptions of Arctocephalus forsteri, see Jones (1925a:15; 1925b: 377-378), Clark (1875), Hector (1871), Webb (1871), Hutton and Drummond (1904: 38), Thomson (1921: 75), Sivertsen (1954: 45ff), Sorensen (1969a: 7) and King (1969). Measurements given by these authors are often not defined, and only recent ones will be cited here. Falla (in Sorensen, 1969b: 61-62) states that males reach a length of 80 inches (203cm) by eight years of age, and that females attain a maximum of 50 inches (127cm). I measured an adult male curvilinear length (as defined by the American Society of Mammalogists, Committee on Marine Mammals, 1967) of 77 inches (195cm), and the curvilinear lengths of two adult females: 49 inches (124cm) and 54 inches (136cm). There are few published records of weights of this species. Hector (1871: 196) gave figures for a large male, and a large female, of 258 pounds (117Kg) and 208 pounds (94Kg), respectively. Thomson (1921: 75) reported weights for males of 260 pounds (118Kg) and over, and for females from 200 to 220 pounds (91 to 100Kg). The largest weight recorded, as far as I am aware, is that of a male who weighed 270 pounds (122Kg) (King, 1964: 35). I collected an old adult male

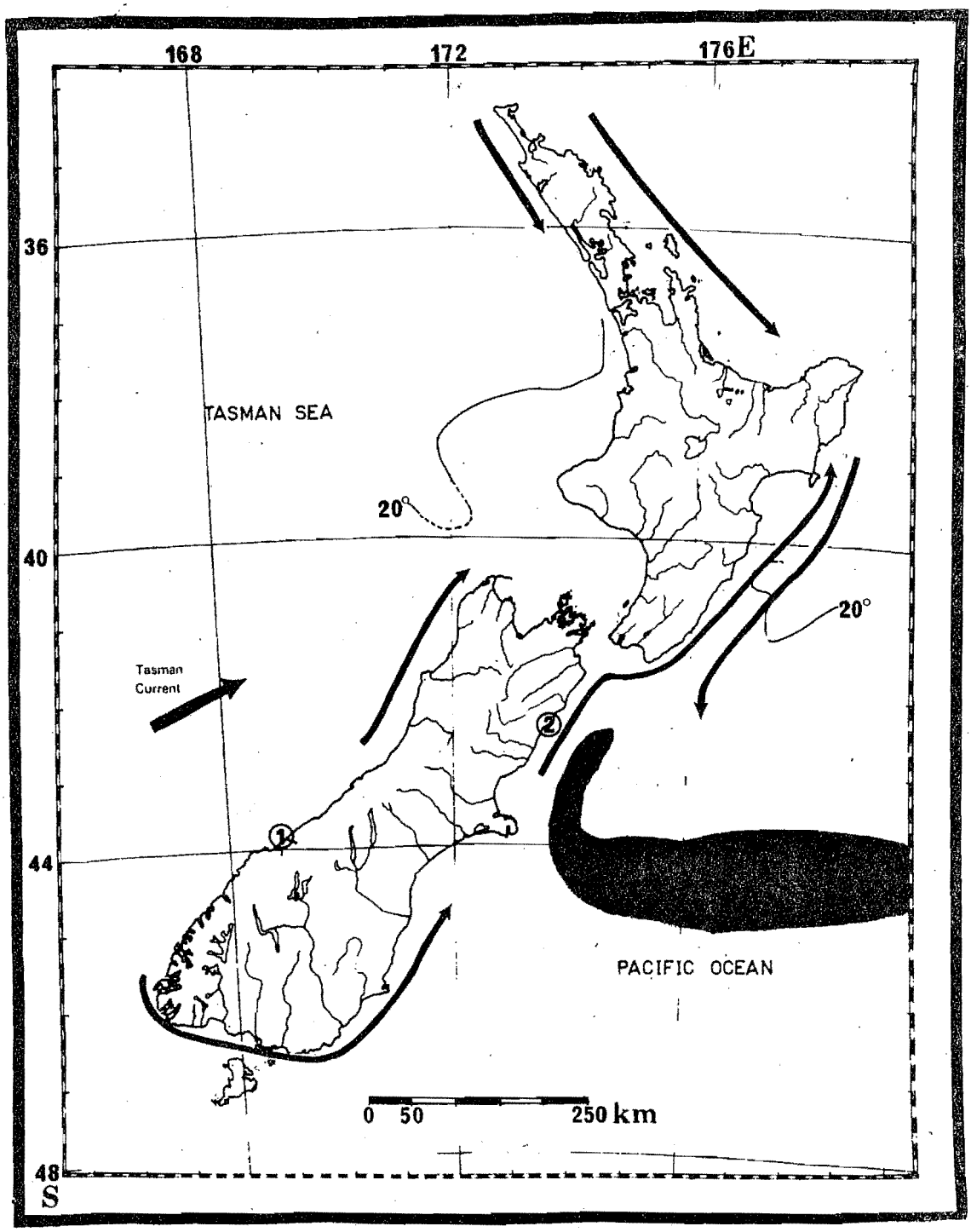
at Kaikoura, on 13 October, 1970, who weighed 296 pounds (134Kg). He was rather small, in comparison to the large territory-holders observed on the Open Bay Islands. It is during the early summer that adult males are heaviest, for they have deposited fat reserves prior to establishing territories and fasting (Howell, 1930: 142). It would not be surprising if large males weighed up to, or even in excess of 400 pounds (181Kg), at the commencement of the breeding season. The female weights reported by Hector and Thomson are unusually large. A very old female (non-pregnant) shot at Kaikoura on 14 October 1970 weighed 82 pounds (37Kg); a pregnant female shot on the Open Bay Islands on 30 November 1970 weighed 77 pounds (35Kg) when her full-term foetus and placenta were removed. Both females were medium in size, and large females must very rarely exceed 175 pounds (about 79Kg). The average weight of mature females is probably between 80 and 110 pounds (36 to 50Kg), yielding a mature male: female weight ratio of about 3.5:1.

E. Habitat.

Cold water currents play an important role in determining the distribution of otariids (see King, 1964: 87-89; R. W. Rand, 1956a: 7, 1967: 3-4; Davies, 1958). Few pinnipeds inhabit waters warmer than 23°C (Peterson in Peterson and LeBoeuf, 1969: 79), and New Zealand coastal waters are considerably cooler than this (see Garner, 1961 and Figure 1). The distribution of A. forsteri in New Zealand waters is undoubtedly influenced by many factors, including topography of hauling-out locations, air temperatures, water temperature, water currents, and food availability.

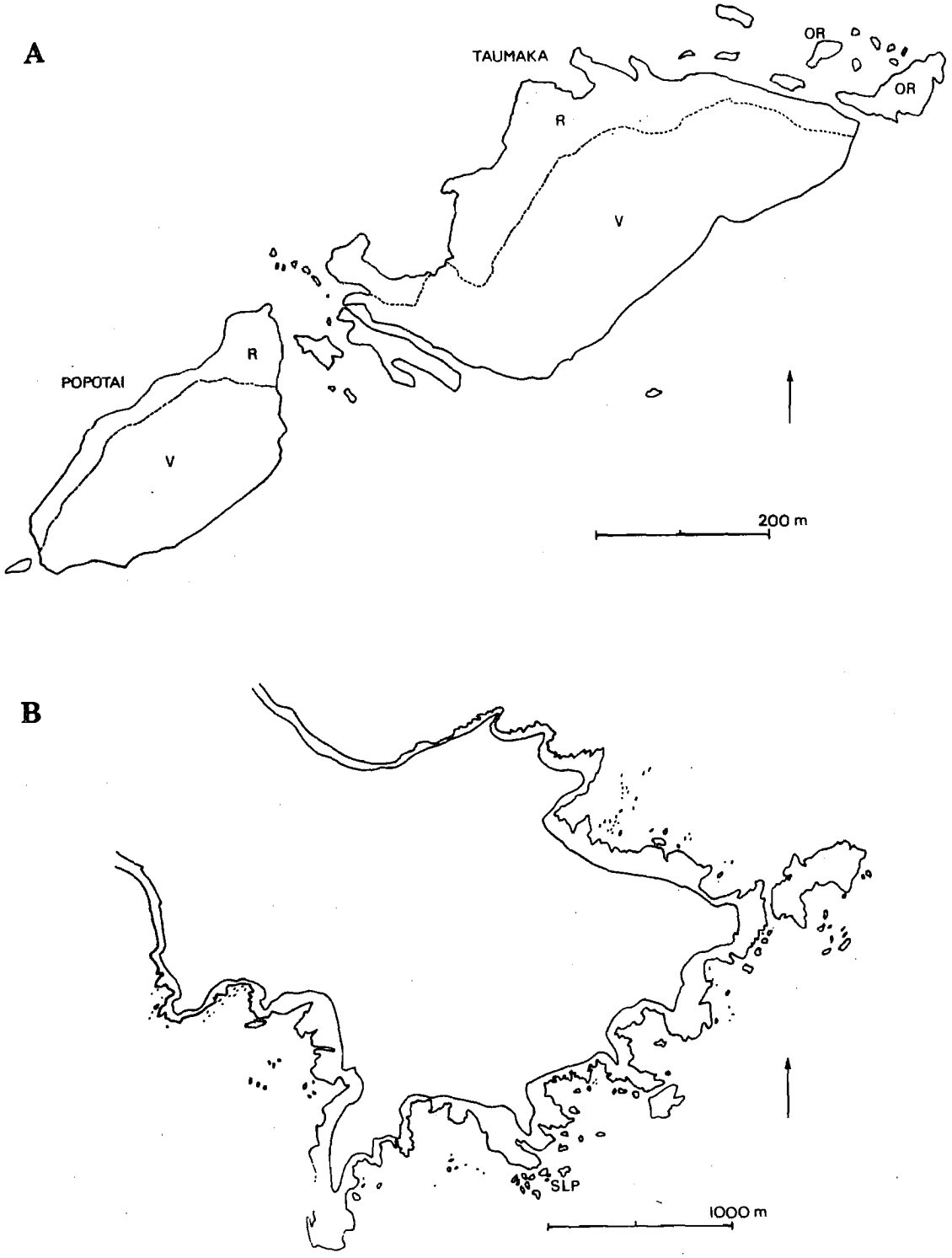
The Open Bay Islands lie in a region of relatively warm water, subject to the influence of the Tasman Current

1. Map of New Zealand, showing major offshore coastal currents, the February 20°C surface isotherm, the sub-Tropical convergence (shaded), and the study areas (1- Open Bay Islands; 2- Kaikoura Peninsula) (After Brodie, 1960 and Garner, 1961).


168
172
176E
36
40
44
48
S
TASMAN SEA
20°
20°
Tasman
Current
PACIFIC OCEAN
0 50 250 km

2.A. Map of the Open Bay Islands. V-vegetated parts; R-breeding rocks; OR-outlying reefs censused each morning.

B. Map of the Kaikoura Peninsula, indicating the location of Sugar Loaf Point (SLP).


A
TAUMAKA
OR
OR
R
V
POPOTAI
R
V
200 m
B
SLP
1000 m

(Figure 1). The Kaikoura coast is subject to the cool, low salinity water of the Southland Current (R. A. Heath, pers. comm.). Fluctuations in sea water temperature off Kaikoura range over about 7°C annually (Heath, 1970: 223), but a fluctuation of 5°C has been recorded within a 24 hour period (Heath, 1970).

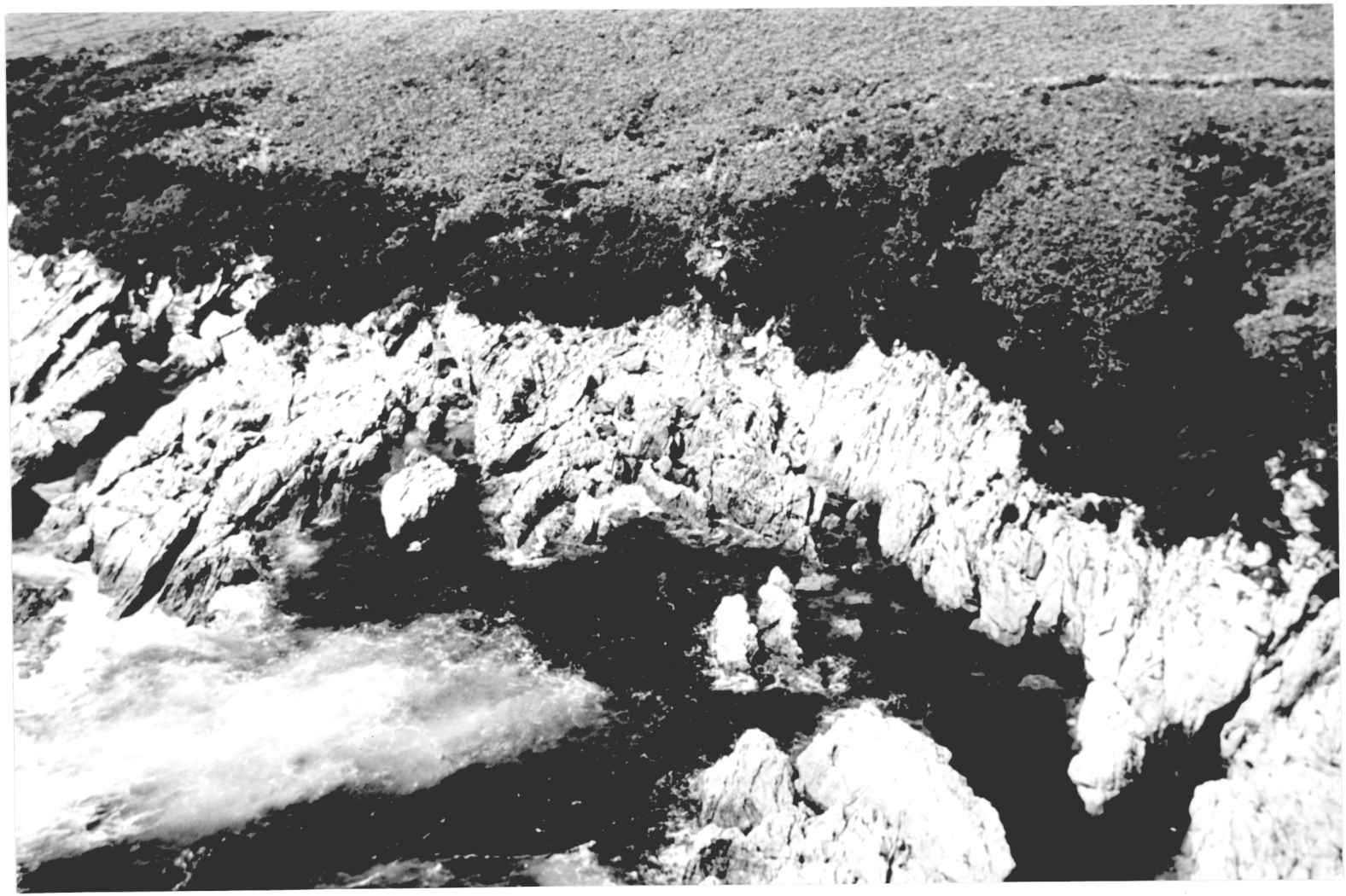
Southern fur seals breed on rocky beaches, in caves, and on coastline characterized by many topographical irregularities and large boulders. For the various species see Paulian (1964: 24ff), R. W. Rand (1956b), and Marsallon (1969: 5) (A. tropicalis); Bonner (1968: 31) (A. gazella); R. W. Rand (1967: 2-3) (A. p. pusillus); Peterson et al. (1968: 668) (A. townsendi); Warneke (1966: 46) (A. p. doriferus) and Bartholomew (1966: 43) (A. galapagoensis).

Falla (in Sorensen,1969b: 58) provides a good description of the habitat used by A. forsteri in New Zealand.

At Kaikoura, the seals haul out on the irregular limestone formations, and avoid the pebble beaches. The general configuration of the substrate at Kaikoura, and its relation to the dispersion of the animals, is shown in Plate 3.

The breeding rocks on both of the Open Bay Islands are comprised of shelves of limestone, which slope from the forest to the shoreline, and are broken up by guts and precipitous drops (Plate 1 and Figure 2A). Large boulders are characteristic of the guts (Plate 5A), and also occur on more level and continuous areas (Plates 4C, 6B). Relatively smooth terrain used for breeding is shown in Plates 4A and 4B, and rougher habitats are shown in Plates 4C, 5A and 6.

1. Aerial view of the main and subsidiary study areas. The main observation blind is visible in the upper central portion of the photograph. Note the distinct banding of vegetation behind the breeding rocks.



2. A. Reefs off the northern end of Taumaka. The large distant one was used by a few breeding seals in 1970-71, and many SAMs aggregated there in early summer.

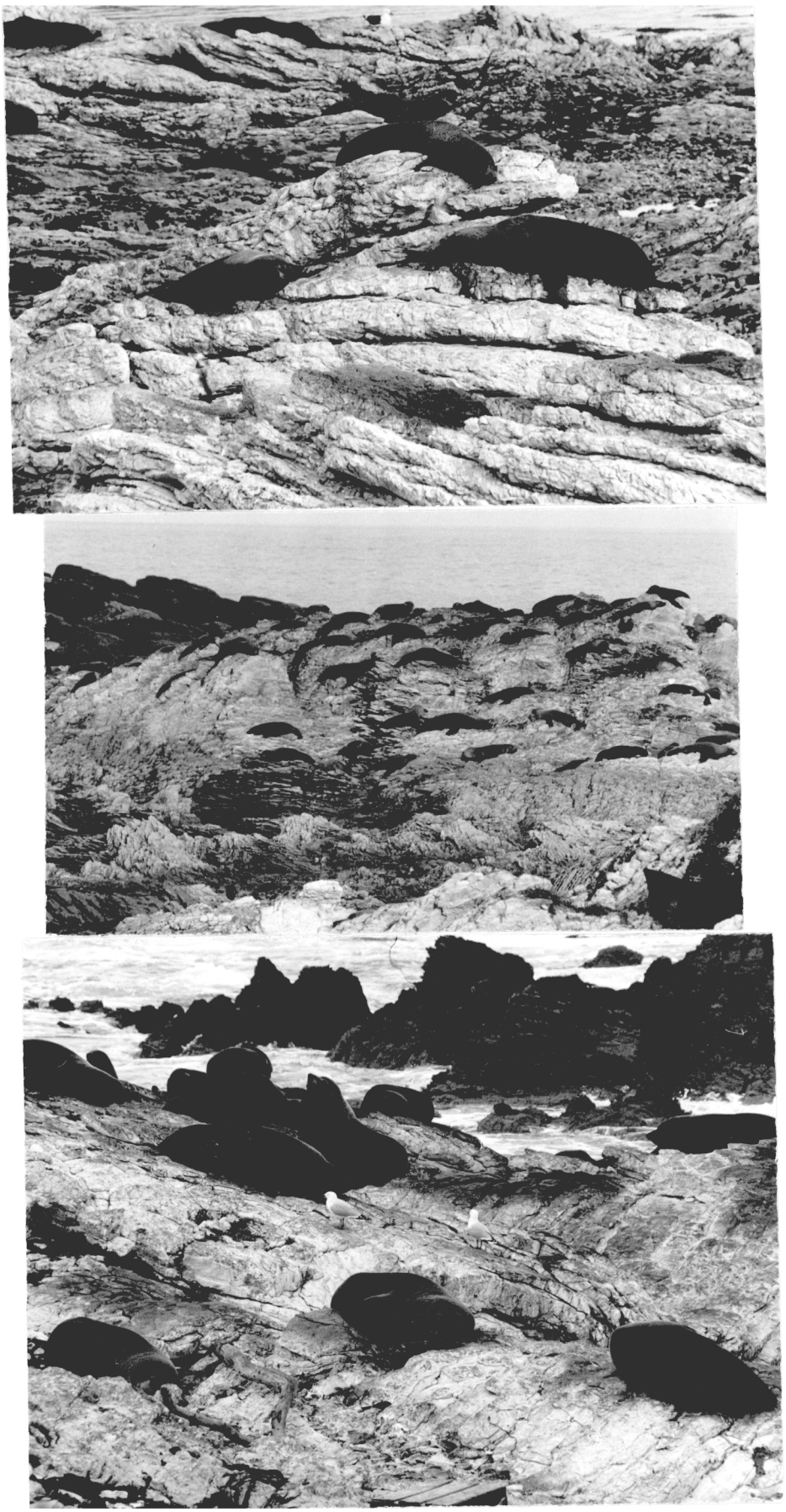
B. Six-month-old pup in the open Hebe forest behind the breeding rocks. Note that the ground is clear of vegetation, due in part to seal movements.

C. Exposed grassy "plateau" on the north end of Taumaka. Juvenile males and some lone females are pictured.

3. A. Typical use of resting ledges by wintering males at Kaikoura (Areas 3).

B. Dispersion pattern imposed on wintering males at Kaikoura by the configuration of the rocks (Area 6).

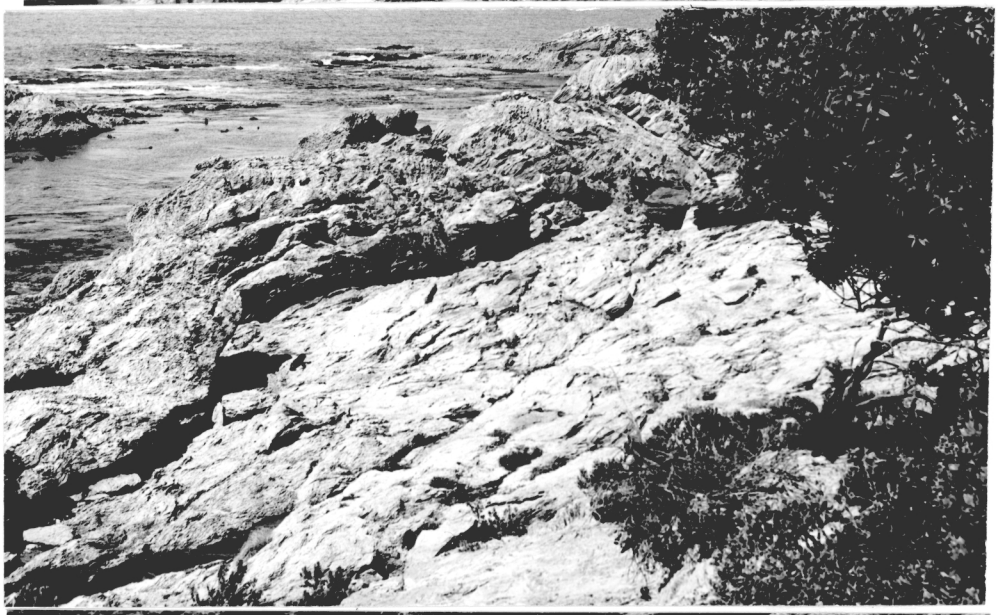
C. Typical dispersion pattern of large wintering males at Kaikoura on an open area. Note the darkly-stained areas, indicating frequent use by resting seals (Area 1).



4. A. Open breeding habitat on the Open Bay Islands. Two territorial males and five females are shown.

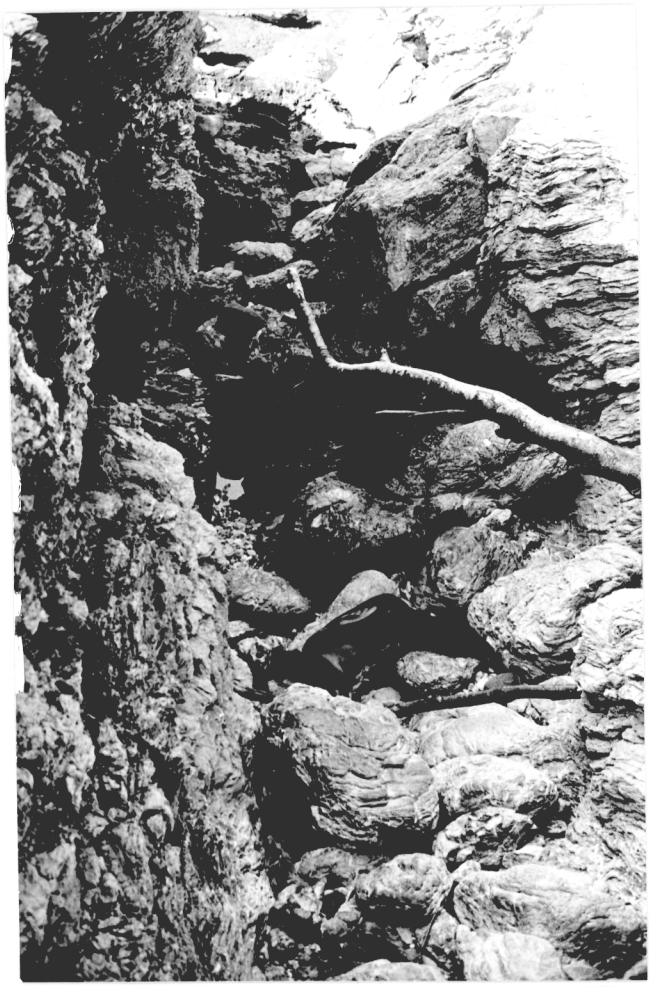
B. Open breeding habitat on the Open Bay Islands. A pup is shown in the left center of the photograph.

C. Typical mélange of rocks in part of a gut used for breeding. A territorial male and three females are visible.



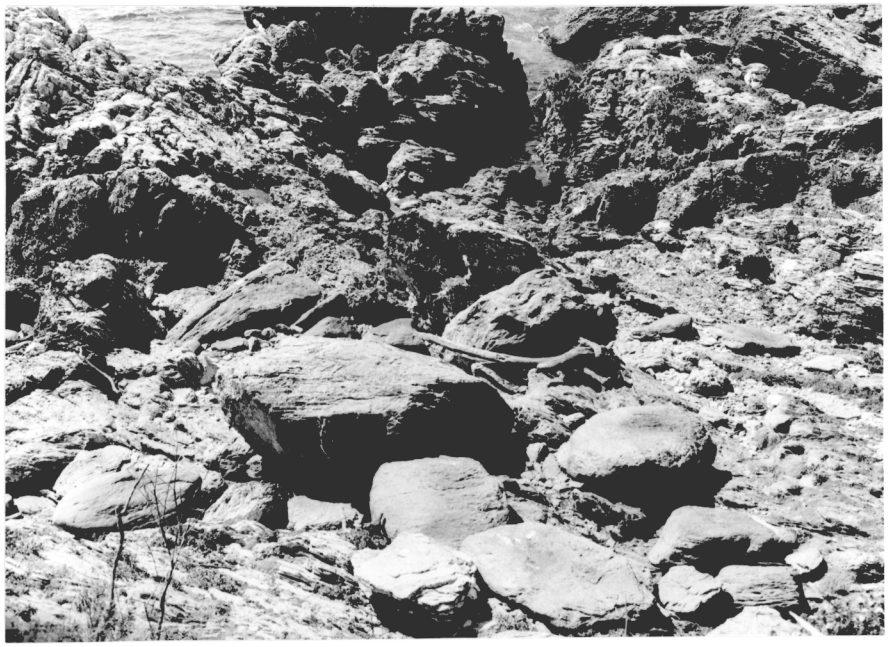
5. A. Breeding habitat on the Open Bay Islands in a narrow gut, flooded during storms. A female nursing her pup is shown in the foreground.

B. Exposed Hormosira-covered reefs off the northwest part of Taumaka. Females, pups, and SAMs rest on the reefs and swim in the channels at low water.



6. A. Distal part of gut (subsidiary study area), showing the extensive use of exposed rocks by females and pups at low water.

B. Part of upper level of main study area on a hot (24°C) sunny day, showing the absence of animals.



Access to vegetated areas is unusual for New Zealand fur seals (Falla in Sorensen, 1969b: 58).

The landward side of Taumaka is typified by high cliffs, but a few jagged large rocks provide resting spots for occasional seals. Off the north end of Taumaka lie some continually exposed, large reefs (Plate 2A) used by immature females, and subadult and untenured adult males when the breeding rocks became occupied. Territorial males on one reef used for breeding sometimes had their territories flanked by non-breeders. The reefs not used for breeding were either awash during stormy weather, or were extremely precipitous with many sharp, jagged edges. At low water, a large area of Hormosira-covered platforms was exposed, and channels running between reefs with associated platforms were heavily used by females with or without pups, subadult males, and in the late summer, lone pups. Plate 5B shows this channel at a moderately low tide, with a few females swimming, and resting on the platform associated with the reef. At times, the number of females swimming in the deep (3-4m) channel, and platform on the far side of it, reached more than 50, and female-pup pairs moved freely back and forth from the island to the platform in late summer.

The side of the island used for breeding is exposed to the prevailing winds, but many parts of the rookery are protected from wind and breaking waves. Only during severe storms is the wind forceful on the level of the rookery.

Accounts of the vegetation are given by Cockayne (1904), and Burrows (in press). Stirling and Johns (1969) briefly described the vegetation and geology of the islands. The large main island (Taumaka), where the observations were carried out, is covered with a dense

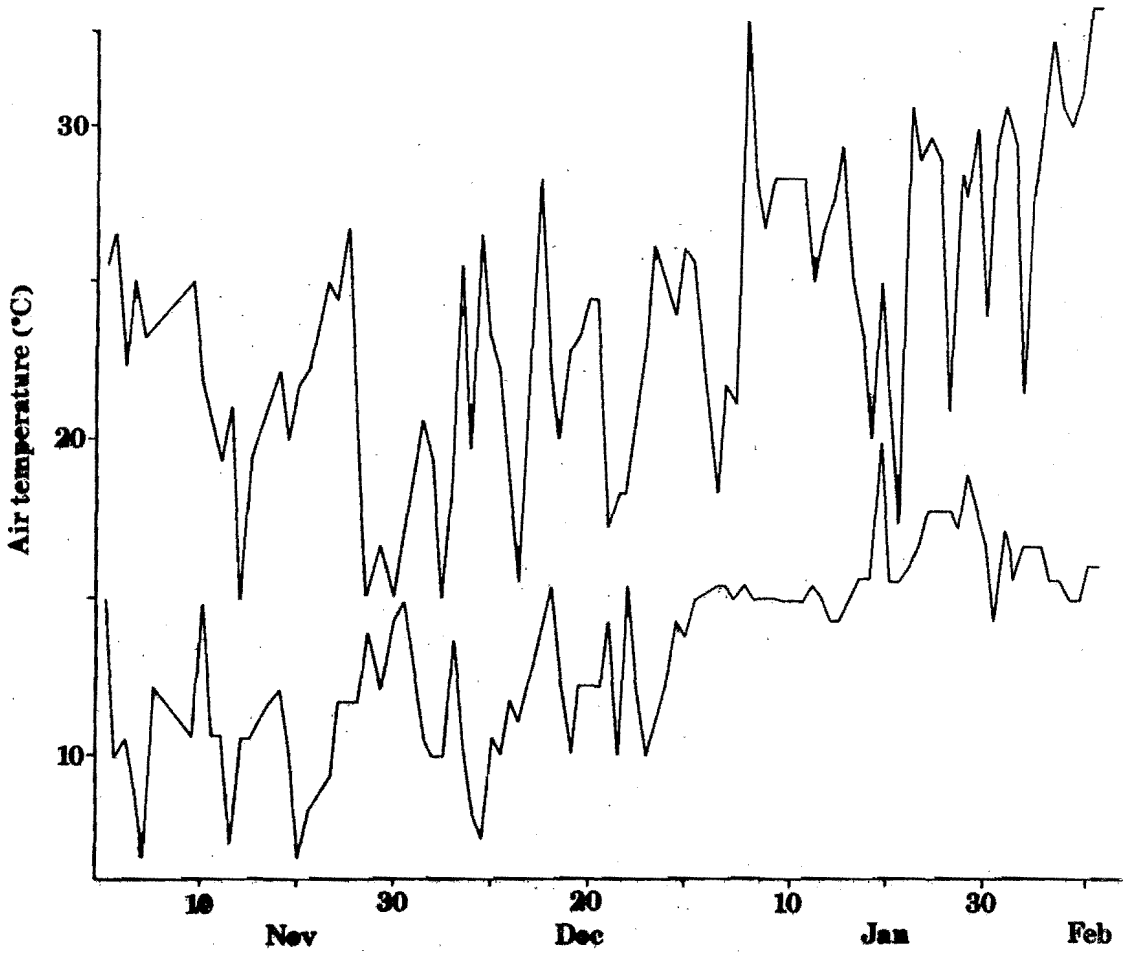
stand of kie-kie (Freycinetia banksii), with an edge of low dense forest consisting chiefly of Hebe elliptica, Schefflera digitata and Fuchsia excorticata (Plate 1). This forest is penetrated by fur seals up to a distance of 50 metres in places (Plate 2B). On the north end of Taumaka is an open, grassy plateau (Plate 2C) which was used extensively by immature animals during the early summer, by females with pups and immatures in late summer, and by young males, females, and pups with and without females, in May 1971. No strictly defined territories impinged on this plateau, but the areas of influence of some territorial males extended onto the plateau and into the forest behind the breeding rocks. An aerial view of the study areas is shown in Plate 1.

The records for maximum and minimum air temperature readings are summarized in Figure 3. The temperature fluctuated erratically until early December, after which a general increase for both maximum and minimum temperatures can be discerned. The curve for maximum temperatures fluctuated drastically, particularly in the second half of the summer, whereas the minimum temperature readings after mid-December were remarkably uniform. This is not surprising, since insolation affected the daytime temperatures, when maxima occurred, but not the nightly minima.

F. Methods.

The locations of the two study areas are shown in Figure 1. Time spent in the field was partitioned as follows: Kaikoura Peninsula (Sugar Loaf Point): 9-17 July, 1970; Open Bay Islands: 17-24 August, 1970; 27 October, 1970 to 13 February, 1971; 26 May - 2 June, 1971. Some seals were collected between 13 and 15 October, 1970 on Sugar Loaf Point, Kaikoura Peninsula, and censuses

3. Seasonal trends in maximum and minimum air temperatures over the main study area.


Air temperature (°C)
30
20
10
10
30
20
10
30
Nov
Dec
Jan
Feb

were made on those days. The total time spent in the field was nearly 20 weeks.

Observations were made in July, 1970 at Kaikoura to become familiar with the animals' general behaviour, to ascertain differences between age classes in dispersion patterns and social behaviour, and to census the wintering males (Figure 2B).

The most prolonged and intensive period of study spanned the summer of 1970-71, on Taumaka (Figure 2A). Two study areas were chosen. A grid of squares each of area $10m^2$, was painted on the main study area with durable, bright orange house paint. The grid did not appear to alter the animals' behaviour. Figure 8A is a map of the main study area, showing the relationship of the grid to the terrain, and indicating place names referred to subsequently. Maps of this sort were used to note locations of individually known animals. All census data were recorded on maps, yielding a day-to-day picture of seasonal trends in dispersion. All interactions between territorial males, male arrivals, male chases, copulations, births, and herding efforts, were recorded on maps and on data sheets.

All territorial males could be readily identified by their own behavioural and morphological quirks. Some yearlings had been previously tagged, or wounded, and were also easily distinguished. Females and pups of the year presented the greatest problem in identification. Marking was attempted by tossing eggs, which had been filled with a fast-acting bleach (Lady Clairol Ultra-Blue with Lightening Booster), which had their shells carefully cracked, and the holes at each end (used for blowing the egg) caulked with putty. Females were too shy to approach within distances at which an accurate strike was assured, and inaccuracies over greater distances

rendered the method impractical. Fifteen pups were marked with the same bleach, and some were still identifiable in late May and early June 1971. When heavily applied, the bleach appeared to irritate the skin of the pups.

Since females could not by dye-marked, I relied on anatomical characteristics for identification, as for adult males (scars, unusual colouration, head shape, missing teeth, characteristics of the vibrissae, etc). Many subadult males (SAMs), particularly large ones, could be recognized by their behaviour and external features. Whenever an unknown animal with recognizable features was seen, a verbal description and pertinent sketches were entered on one side of a 5" x 8" file card, and the date, time, and location of observations on the other side. Subsequent sightings were noted on the same side, and entered on a map.

During the field work in late May and early June, 1971 on the Open Bay Islands emphasis was given to determining the proportions of small males ashore, their relationships with one another, and with females. Censuses were made, and dispersion maps filled out.

CHAPTER II. SEASONAL TRENDS IN POPULATION DISTRIBUTION AND DISPERSION.

A. Introduction.

Most seals have rigidly-timed breeding seasons. The reasons for seasonal geographical shifts of certain classes of seal populations are poorly understood, but during breeding many individuals are excluded from rookeries for sociological reasons. In this chapter, an overview of the annual cycle will be presented, with an analysis of the patterns of space-use by breeding females on the main study area.

B. Seasonal trends in numbers and composition.

1. Kaikoura: Counts of seals on Sugar Loaf Point in 1970-71 were highest in mid-winter and lowest in mid-summer (Table 1). This trend is in agreement with that noted by Stonehouse (1965, 1969). There appeared to be seasonal changes in the proportions of large and small males present, with large males abundant in March, 1971.

Females haul out sporadically at Kaikoura. A single old female was shot there in October, 1970, and a still-born pup was collected on Sugar Loaf Point in September, 1968 (G. C. B. Poore, pers. comm.).

2a. Open Bay Islands: summer 1970-71. Main study area. Adults. Early morning census figures for females, yearlings and territorial males for the two study areas are plotted in Figure 4. Early morning censuses were preferred to evening censuses, because the former were consistently higher and less affected by the weather of the day.

Some territory-holding males were present on the islands in late October, and their numbers increased slowly

TABLE 1:

SUMMARY OF CENSUSES AT SUGAR LOAF POINT, KAIKOURA PENINSULA, 1970-71

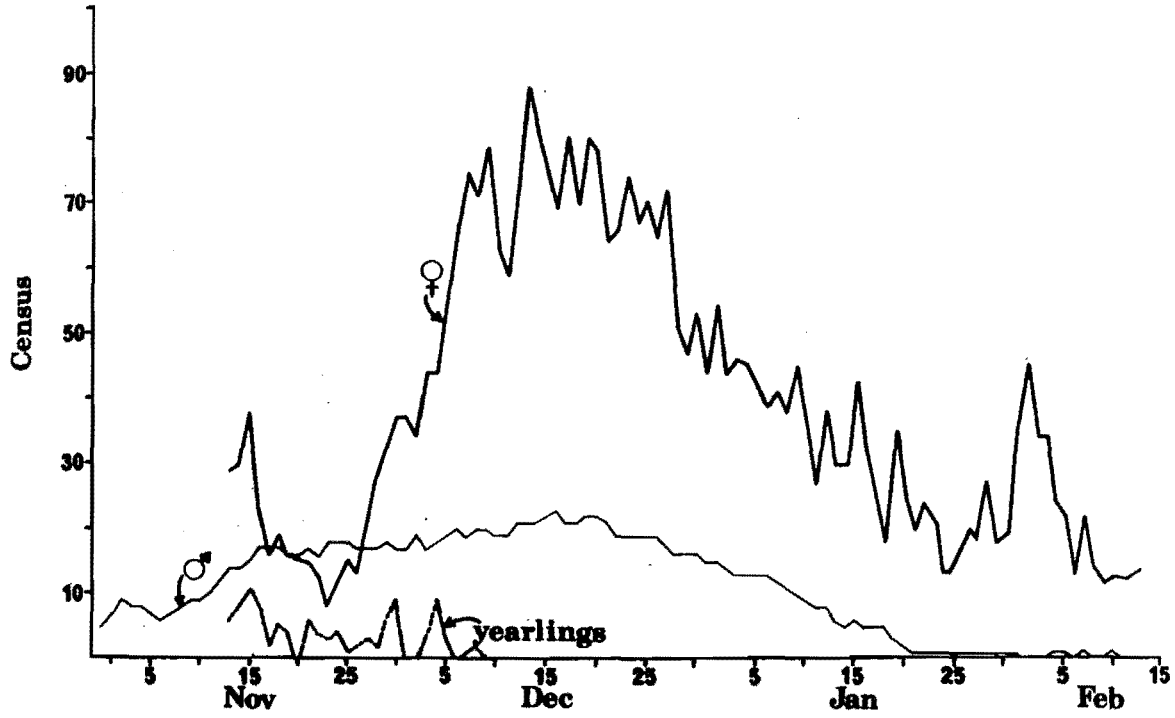
DATE	TIME OF CENSUS	MAXIMUM CENSUS
10 July, 1970	1200	282
11 July, 1970	1550	357
12 July, 1970	0900	375
13 July, 1970	1110	307
14 July, 1970	1200	323
15 July, 1970	1200	301
16 July, 1970	1200	268
17 July, 1970	1000	284
13 October, 1970	1525	94
14 October, 1970	0830	160
15 October, 1970	0940	125
19 December, 1970[1]	-	7
8 March, 1971	1230	170
6 July, 1971[2]	-	550-580[3]
27 August, 1971	1000	156[3]

[1]Censused by M. Miller

[2]Censused by B. Hicks

[3]Only censuses of day

4. Seasonal trends in the numbers of territorial males, females, and yearlings censused each morning on the main study area.


Census
90
70
50
30
10
♀
♂
yearlings
5
15
25
5
15
25
5
15
25
5
15
Nov
Dec
Jan
Feb

until mid-December.

Yearlings, some still nursing, were seen most days until 9 December. There was a number of gaunt starvelings present, but most yearlings appeared to be well-fed. The low number of females ashore during the last half of November may be due to a tendency for pregnant females to feed heavily in the weeks before giving birth. R. W. Rand (1967: 11) noted that females of A. p. pusillus spent increasingly longer periods of time at sea before giving birth. Many pregnant females arrived on the Open Bay Islands in late November, a few days prior to giving birth (see Chapter IV B2). This accounts for the sudden increase in the female census figures after 23 November. Numerous females were present throughout December, for two reasons. First, the period which a female spends on shore with her newborn pup is probably the longest continuous association they ever have together on land. Since births occurred in a brief period, many females were in the post-partum association with their pup simultaneously. Second, pregnant females continued to arrive ashore throughout December. The decline in the numbers of females in late December was due to the lower rate of recruitment of pregnant females, the increased amount of time which mothers were spending away from the rookery feeding, and probably the tendency of females who had lost their pups to stay away. Some A. p. pusillus females with pups spent almost 60% of their time on shore, while some without pups spent less than 30% of their time on land (R. W. Rand, 1967: 49-50). Similarly, Eumetopias females with pups are on shore 63% of the time during the summer, while those females without pups are ashore only 47% of the time (Gentry, 1970: 67).

The intense competition among adult males for space on the rookery, and the strategic and psychological

advantages of holding a territory when confronted by challenging males, are sufficient to explain the large numbers of males on station in mid to late November, when few females were present. The tendency to compete for territories even before females are present in large numbers is characteristic of adult male otariids, (e.g. see Peterson, 1965: 25ff on Callorhinus; Paulian, 1964: 34-35 on A. tropicalis; R. W. Rand, 1967: 15 on A. p. pusillus and Gentry, 1970: 91 on Eumetopias). Unlike the studies cited, the number of territories on the Open Bay Islands continued to increase while the number of females was very high. Thus, there may be a stimulatory effect of the presence of females on untenured adult males, inducing them to compete for territories.

The only other fur seals which have been reported to nurse their pups for as long as a year are A. pusillus (R. W. Rand, 1955: 726; Stirling and Warneke, 1971: 240) and Australian A. forsteri (Stirling, 1971a: 246-247). It is likely that a proportion of the yearlings of New Zealand A. forsteri travel with their mothers (Gwynn, 1953: 5-6; Stonehouse, 1965: 18; Csordas and Ingham, 1965: 92). Females swimming with yearlings have been observed in Zalophus (Peterson and Bartholomew, 1967: 44) and Eumetopias (Gentry, 1970: 60), and a possible case of maternal solicitude for a 6 or 7 month old Halichoerus pup has been reported (Boyd, 1955). Maintenance of the female-pup bond up to and beyond a year is typical of the sea lions Neophoca (Marlow, 1968: 42), Otaria (J. E. Hamilton, 1934: 298), Zalophus (Peterson and Bartholomew, 1967: 44), and Eumetopias (Sandegren, 1970: 74; Gentry, 1970: 63). No female A. forsteri on the Open Bay Islands was observed to nurse both a pup and a yearling, and no pregnant females were seen to nurse yearlings. The abandonment of the Open Bay Islands by the yearling class

may be due to movement away from the rookery with mothers, increasing competition with the burgeoning female population for food resources, or weaning. Territorial males were generally tolerant of yearlings, and the presence of males is not a likely contributory cause to the decline of the yearling class ashore.

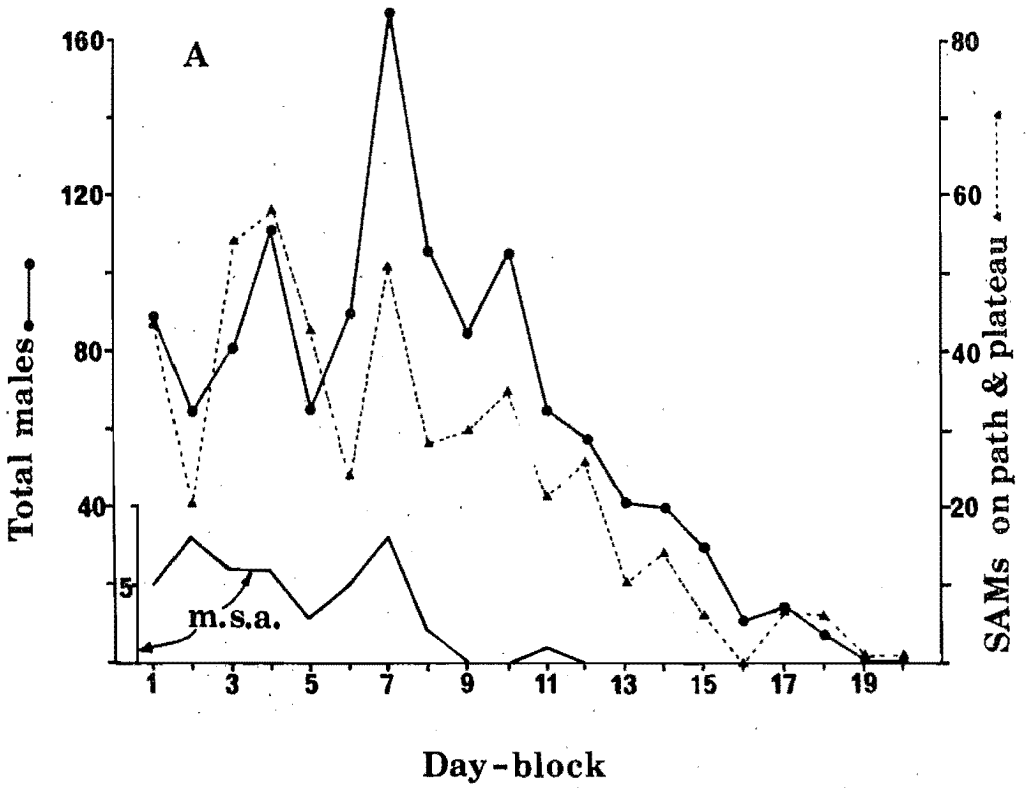
2b. Subadult males (SAMs). The SAM population on the trail, the plateau, and the outlying reefs was censused each day between 0400 and 0700 hours (Figure 5A) (for dates corresponding to day-blocks, see Appendix B).

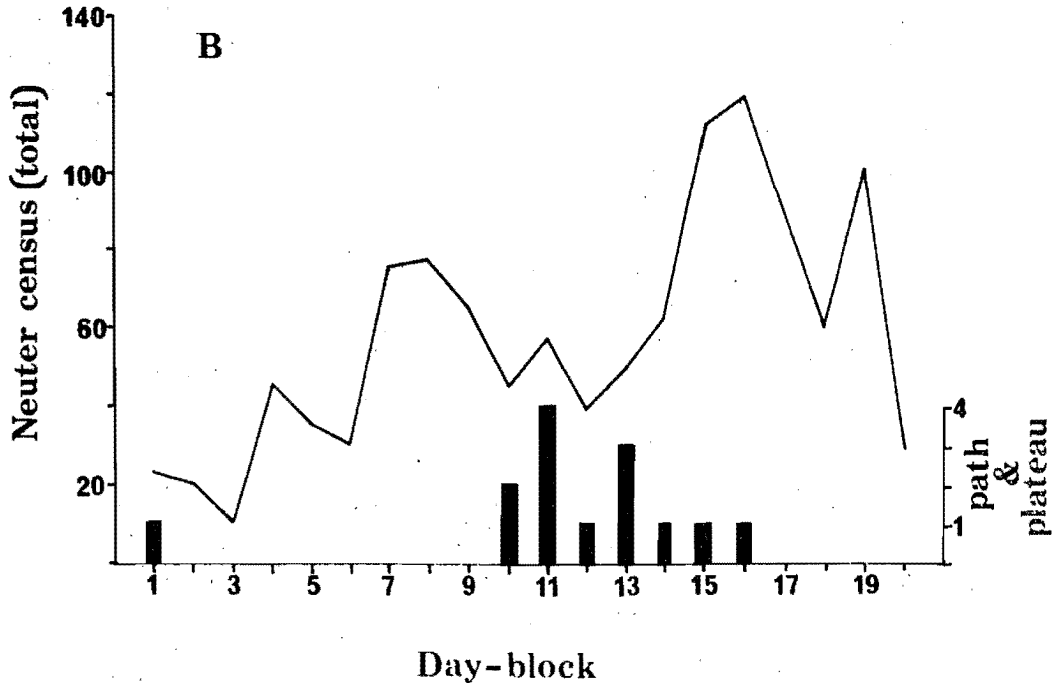
Seals encountered on the trail and plateau could be unequivocally classed as SAMs or adult males, but it was difficult to distinguish between these classes on the outlying reefs. A few territory-holding males were present on the reefs, and their occasional inclusion as SAMs accounts for part of the difference between the curves for 'total males' and 'total SAMs' in Figure 5A. The similarity in the two curves suggests that errors in distinguishing the classes were minor.

The number of SAMs fluctuated at a high level until day-block 10, then decreased steadily. The curve in the bottom left of Figure 5A indicates that the number of SAMs present on the main study area (and by extension, on the breeding rocks) was high until day-block 7. Thus, the trends for the SAM population, based on censuses made on non-breeding areas of the island, are obscured until about day-block 8 due to the use of breeding rocks by SAMs. The decline apparent after day-block 10 may simply be a continuation of a decline present throughout the summer, which was obscured by changes in the patterns of space-use by SAMs.

5.A. Seasonal trends in the number of males censused on the outlying reefs, path, and plateau (total males), the path and plateau only (SAMs), The numbers of SAMs counted on the main study area (m.s.a.) each morning are shown in the lower curve.

B. Seasonal trends in the numbers of neuters censused on the outlying reefs, path, and plateau (total), and the path and plateau only.


A
Total males
SAMs on path & plateau
m.s.a.
Day-block


B
Neuter census (total)
path & plateau
Day-block

Spatial segregation of non-breeding males from breeding colonies is characteristic of otariids, and is due to the intolerance of territorial males toward all other males except pups and yearlings. Crawley (in press) has noted the segregation of non-breeding A. forsteri bulls from the breeding concentrations on the Snares Islands. Juveniles (predominantly males) of A. gazella are present throughout the breeding season on South Georgia, behind and away from the breeding beaches (Bonner, 1968: 65). Non-breeders increase in numbers toward the end of the summer in Callorhinus (Peterson, 1965: 21-22) and A. p. pusillus (R. W. Rand, 1956a: 22). At a colony of A. forsteri in Australia, the numbers of non-breeding males changed little over a breeding season (Stirling, 1971a: 246). Thus it appears that the presence of non-breeding adult males and SAMs around fur seal rookeries during the summer is influenced by a number of factors, with no apparent relationship to taxonomic affinities.

2c. Neuters. When seals could not be sexed, they were listed as 'neuters'. A general increase in the number of neuters occurred over the summer (Figure 5B). That this class was comprised largely of females is suggested by the following evidence. When the outlying reefs were visited and censused, most individuals were females. For example, on 31 October two females were seen there, none on 2 or 3 November, 18 on 20 December, 17 on 13 January, 20 on 4 February and 27 on 5 February. Only two pups were known to have been born on the reef, so the females present can not be accounted for in terms of births. Second, the population of identifiable SAMs decreased over the summer (Figure 5A), and it can be inferred that the population of male neuters also declined. Finally, female BT, who gave birth on the main study area, and whose pup died, was

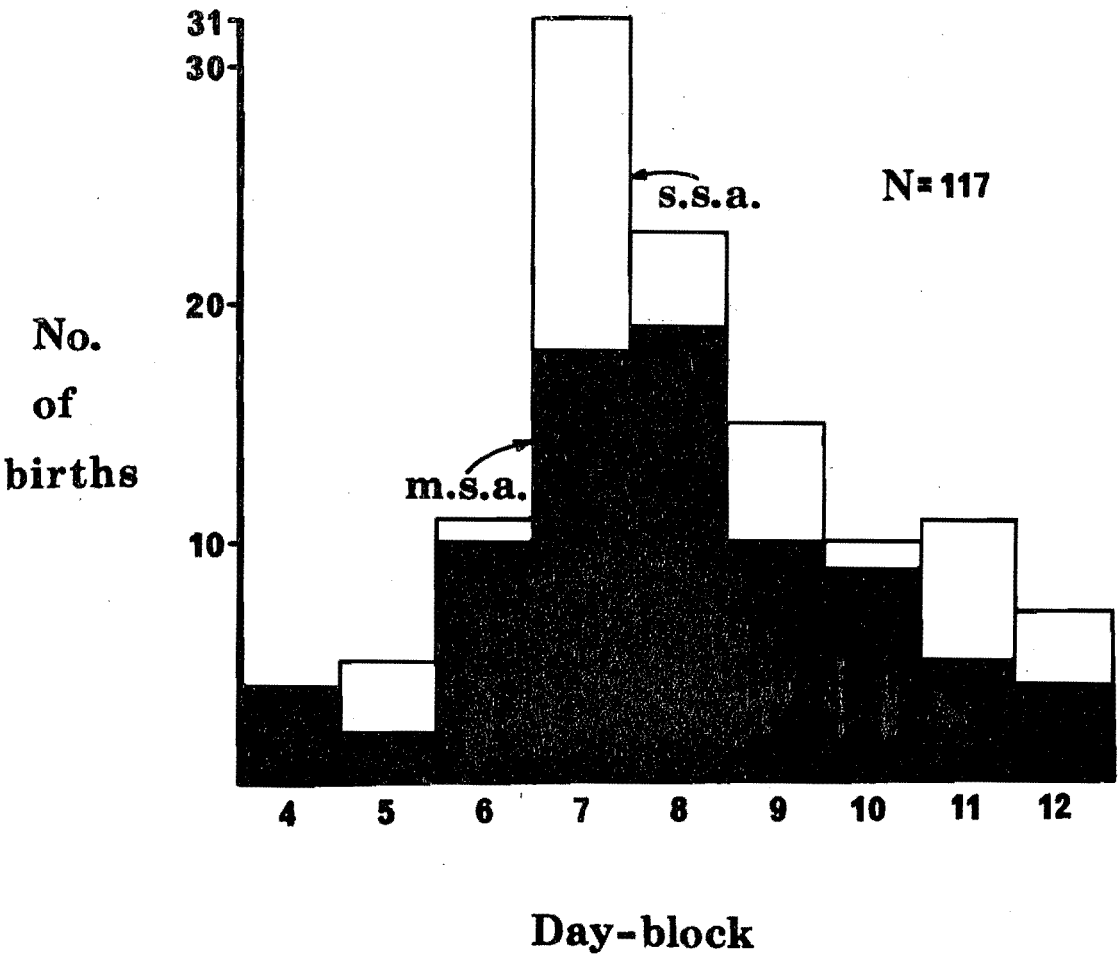
observed on the outlying reefs twice in the weeks following the death of her pup. This suggests that females who lost their pups formed a proportion of the neuter class on the outlying reefs. Abegglen and Roppel (1960: 75) state that on areas adjacent to the rookeries, female Callorhinus increase in numbers as the summer progresses.

2d. Main study area: births. A stillbirth occurred on 31 October, and live births occurred over a 42 day period, from 18 November to 29 December (Figure 6). The mean date of pupping was 9 December ($N = 117$, $s^2 = 96.3$). More than three-fourths of the births (76.9%) occurred between 29 November and 19 December. The seasonal distribution of births followed a normal curve ($D = 0.10216$)*.

Some other sedentary species of fur seals have rigidly timed breeding seasons. Births in an Australian colony of A. forsteri occurred from 29 November to 22 January (55 days) (Stirling, 1971a: 247). R. W. Rand (1967: 26) reported that pups of A. p. pusillus are born from October to December, with full-term pups appearing in early November, (R. W. Rand, 1955: 723). Pups of A. p. doriferus are born from late November to mid-January (Warneke, 1966: 46). In contrast, A. galapagoensis (Heller, 1904: 247) and Z. c. wollebaeki (Snow in Orr, 1967: 63) have poorly-defined breeding seasons. Some comparable figures for more seasonally restricted otariids are: Callorhinus, 15 June to 10 August (Peterson, 1965: 133); Eumetopias, late May to late June in Alaska and British

* Data were routinely screened by Program A-1, Zoology Department, University of Canterbury. For abbreviations and methods of testing here and elsewhere in the text, see Sokal and Rohlf (1969).

6. Seasonal trends in the numbers of births occu on the main (m.s.a.) and subsidiary (s.s.a.) study areas.


31
30
20
10
No.
of
births
s.s.a.
N= 117
m.s.a.
4
5
6
7
8
9
10
11
12
Day-block

Columbia (Mathisen, Baade, and Lopp, 1962: 469; Pike and Maxwell, 1958: 5); and mid-May to early July in California (Gentry, 1970: 53-54). Among phocids, the harbour seals studied by Harrison in Britain showed amazing seasonal synchrony: over 13 years, 85% of the pups were born between 19 and 23 June (Harrison, 1963: 101). The Southern elephant seals studied by Carrick et al. (1962: 150) had over 80% of the births in a 3 week period, even though, as for A. forsteri on the Open Bay Islands, some were present throughout the year (op. cit.: 152). The Hawaiian monk seal breeds from early January to early June (Kenyon and Rice, 1959: 236). The duration and timing of breeding seasons in Halichoerus are well documented (for a review of geographical differences, see Curry-Lindahl, 1970: 17). Breeding in this species lasts up to 2 months in the Southern Inner Hebrides (Hewer and Backhouse, 1960: 172-173), 4 months on North Rona (Boyd, 1967: 20), and $2\frac{1}{2}$ months on the Farne Islands (Coulson and Hickling, 1964: 495). In summary, the duration and timing of the breeding season varies between and within species, but only tropical or near-tropical sedentary forms have protracted breeding seasons.

3. Open Bay Islands: May-June 1971. Numerous SAMs were ashore on the Open Bay Islands between 26 May and 2 June, 1971 (Table 2). Most SAMs were very small, and difficult to distinguish from females. Few adult males were present, and some very small females were recorded. A similar situation prevails in Australian A. forsteri (Stirling, 1971a: 246).

TABLE 2:

SUMMARY OF CENSUS DATA, 26 MAY - 2 JUNE 1971,
OPEN BAY ISLANDS

	N	%
ADULT MALES	6	1.0
SAMS	112	19.0
FEMALES	173	29.3
PUPS	299	50.7
TOTAL:	590	100.0

4. Discussion: seasonal timing. It is apparent that A. forsteri on the Open Bay Islands exhibits marked seasonal synchrony in territoriality and dates of pupping. The use of a seasonal cue to serve as a 'trigger' to initiate sexual development and physiological readiness is a fruitful strategy where the optimum time for raising young is predictable, and where 'physiological prognostication' of future conditions is imperative because of a necessary preparatory phase (e.g. gestation) (Schreiber and Ashmole, 1970: 386). These conditions are fulfilled for many seasonally breeding otariids, where food supply around the rookeries, air temperature, weather, and day-length, vary predictably throughout the year.

The use of day-length as a trigger for implantation of the blastocyst has been suggested by Harrison (1963: 109ff). Pinnipeds have the largest pineal body of all mammals (Cuello and tramezzani, 1969: 161), and recent researchers have suggested that its unusual size may be related to seasonal synchrony in breeding (for Leptonychotes, see Cuello and Tramezzani, 1969; for Callorhinus, see Elden, Keyes, and Marshall, 1971) (cf. Quay, 1969).

The cue used for implantation of the blastocyst must by exogenous. This is because copulations occur over a greater period of time than do births, for various pinnipeds. For example, nulliparous A. p. pusillus females sometimes ovulate before the breeding season (R. W. Rand, 1955: 721-722), and nulliparous Callorhinus females may ovulate up to 2 months later than do other mature females (Craig, 1964: 791). Stirling (1971a: 246) recorded copulations occurring about 3 weeks before the first births in Australian A. forsteri. On the Open Bay Islands, copulations were observed from 13 November to 18 January ($\bar{Y}$ = 16 December, N = 54, s^2 = 144.1), but the

associated variance was not significantly greater than that for the dates of birth ($F_s = 1.50$, n.s.). However, it was difficult to obtain data on copulations in the early summer, and it is probable that the variance for the dates of copulation is in fact greater than that for the dates of birth. Hence, the date of implantation for this species, as for other pinnipeds, is not set by the date of copulation, but by some exogenous factor (see Carrick et al. 1962: 148ff).

If the present timing of breeding in different populations of pinnipeds is being maintained by normalizing selection, then identification of the selective agents involved should explain the observations. If, on the other hand, the environmental forces which moulded seasonal synchrony in breeding were sufficiently strong to cause a change in the response of the population from a variant, exploitive one, to a fixed, obligatory one, then removal of such selective pressures may not be accompanied by an associated response in the population (see Mayr,1963: 610-612; Fairbairn, 1970: 32-34). The latter is unlikely to prevail in the seasonal timing of reproduction in pinnipeds: grey seals show geographical differences in the duration and dates of breeding, and northern elephant seals have retained similar dates of breeding to their southern hemisphere congener. Therefore, it is assumed that the present seasonal timing exhibited by pinnipeds is being maintained by normalizing selection, and is proximally adaptive (see Cain, 1964).

Belkin (1966) and Ling (1969) have suggested that interspecific intolerance could affect breeding seasons in pinnipeds. There is no evidence, current or historical, to indicate that interspecific competition was important in modifying or maintaining the breeding regime of A. forsteri in New Zealand.

C. Adult dispersion, and competition for space among females.

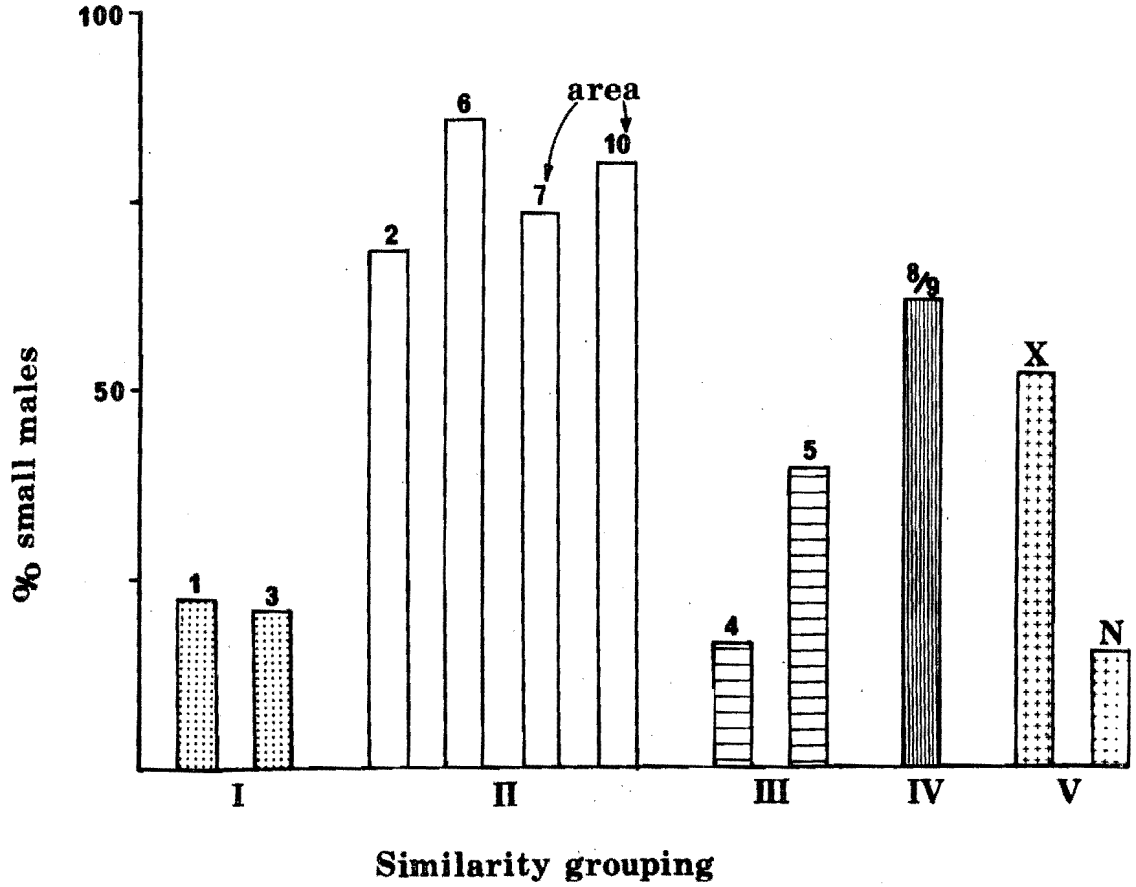
1. Kaikoura: Winter dispersion of males. The spatial segregation of large and small males is a striking characteristic of the aggregation of wintering males at Kaikoura. Absolute and relative numbers of large and small males on each region of Sugar Loaf Point were determined at each census (Figure 7).

Mainland regions 1 and 3 attracted mainly large males; recurrent human disturbances may have permanently driven away the shyer, small males, although no disturbances occurred during the 8 days of observation. Areas 2, 6, 7, 8/9 and 10 were populated mainly by small males. Large males were commonest where there were broad ledges or flat areas suitable for hauling out (Plates 3A, 3C), and where wave action and disturbance by active, playing seals were minimal. Small males predominated on areas too rugged and angular for use by large males (areas 2, 6, 7, 10) and areas with ready access to the sea (reefs 8/9, X). The latter were used extensively for play. The relatively steep outer rock N was used primarily by resting large males.

2. Open Bay Islands: competition for space and dispersion patterns of females. This section deals with space-use patterns of females only. The movements of territorial males were determined by their neighbours, and the prescence of females.

The distribution and dispersion of breeding females affects that of territorial males. If females are intolerant of the proximity of one another, this may limit the number of copulations a territory-holder can achieve. If females crowd tightly, a negative density-dependent

7. Regional differences in the proportion of small males occurring on Sugar Loaf Point. Areas 1,3: moderate to smooth topography, restricted access to sea; Areas 2, 6, 7, 10: rugged, angular, or steep topography, reasonable access to sea; Areas 4,5: moderate topography, low to water; Areas 8/9: smooth, low reefs; Areas X, N: smooth, high reefs.


100
50
% small males
area
1
3
2
6
7
10
4
5
8/9
X
N
I
II
III
IV
V
Similarity grouping

factor (see T. H. Hamilton, 1967: 42) could operate through pup mortality, lessening a male's genetic influence. A shortcoming of the present study on competition for space among females is the paucity of data on individually recognizable females. Data based on birth dates, censuses, and time on land around birth, are used in the following analysis. Arbitrarily-defined birth regions on the main study area are illustrated in Figure 8B.

2a. Competition for space: evidence from female censuses. Individually recognizable females were seen within particular birth-regions from 1 to 3 days before birth, and for as long as 12 days after birth (Table 3). For females with reliable and complete records, the mean time spent within a birth-region after birth was 9.24 days. These females observed from their arrival, spent 10, 12 and 12 days ($\bar{Y}$ = 11.33 days) within the regions where they pupped. The values in the last column of Table 4 are probably underestimates, because of the difficulty in identifying females when they took up pre-partum residence in a birth-region. For the present analysis, it is assumed that females entered a birth-region 3 days before parturition and spent 10 days there after birth. A series of figures for 'theoretical space occupancy' can then be calculated, based on this assumption, and using data on the dates of birth for each region. If the maximum number of females ever recorded at one time within each birth-region is an estimate of 'saturation' conditions, the figure ((maximum female census) - (theoretical space occupancy)) provides an estimate of the amount of space still 'available'. The curve generated will be termed the 'theoretical space availability curve', and is shown for each birth-region in

TABLE 3:

SUMMARY OF TIME SPENT BY INDIVIDUAL FEMALES WITHIN BIRTH REGIONS

Female	Date Pupped	Days in birth region pre-partum	Days in birth region post-partum	Total days in birth region
A	3 Dec.	-	10	10+
ACE	16 Dec.	1 (+?)	8	9 (+?)
AR	20 Dec.	3	9	12
BBC	20 Nov.	-	10	10+
BT	14 Dec.	-	10	10+
CL	20 Nov.	3	9	12
CR	17 Dec.	1	9	10
14	30 Nov.	-	9	9+
19	2 Dec.	-	8+	8++
29	4 Dec.	-	8	8+
38	6 Dec.	-	12	12+
44	7 Dec.	-	10	10+
50	8 Dec.	-	7+	7++
74	18 Dec.	-	9	9+
FB	19 Nov.	-	6	6+
F2	9 Dec.	-	8	8+
LP	20 Nov.	-	7+	7++
PB	17 Dec.	-	11	9+
UM	3 Dec.	-	11	11+
WV	16 Dec.	-	8	8+

TABLE 4:

REGIONAL DIFFERENCES IN DATES OF PUPPING,
OPEN BAY ISLANDS 1970-71

	Mean date of pupping	S.E.	S^2	N
MAIN STUDY AREA	8 December	1.050	89.38	81
SUBSIDIARY STUDY AREA	11 December	2.017	126.15	31
MAIN STUDY AREA: I [1]	9 December	2.145	119.63	26
MAIN STUDY AREA: II [1]	7 December	1.631	95.76	36
MAIN STUDY AREA: III [1]	10 December	1.142	38.37	19
MAIN STUDY AREA: II [1] & III [1]	8 December	1.180	76.63	55
TOTAL:	9 December	0.907	96.25	117

[1] Birth-regions

TABLE 5:

F-RATIOS , BASED ON DATA IN TABLE 4 (LEGEND AS IN TABLE 4)

Comparison	F_s	P
MAIN vs. SUBSIDIARY STUDY AREAS	1.31	n.s.
MAIN STUDY AREA I vs. II & III	1.56	n.s.
MAIN STUDY I vs. II	1.25	n.s.
MAIN STUDY AREA I vs. III	3.12*	$0.01 < P < 0.02$
MAIN STUDY AREA II vs. III	2.50*	$0.02 < P < 0.05$

8. A. Map of the main study area, showing place names and the general configuration. The grid shown is of squares $10m^2$.

B. Map of the main study area, showing the birth regions referred to in the text.

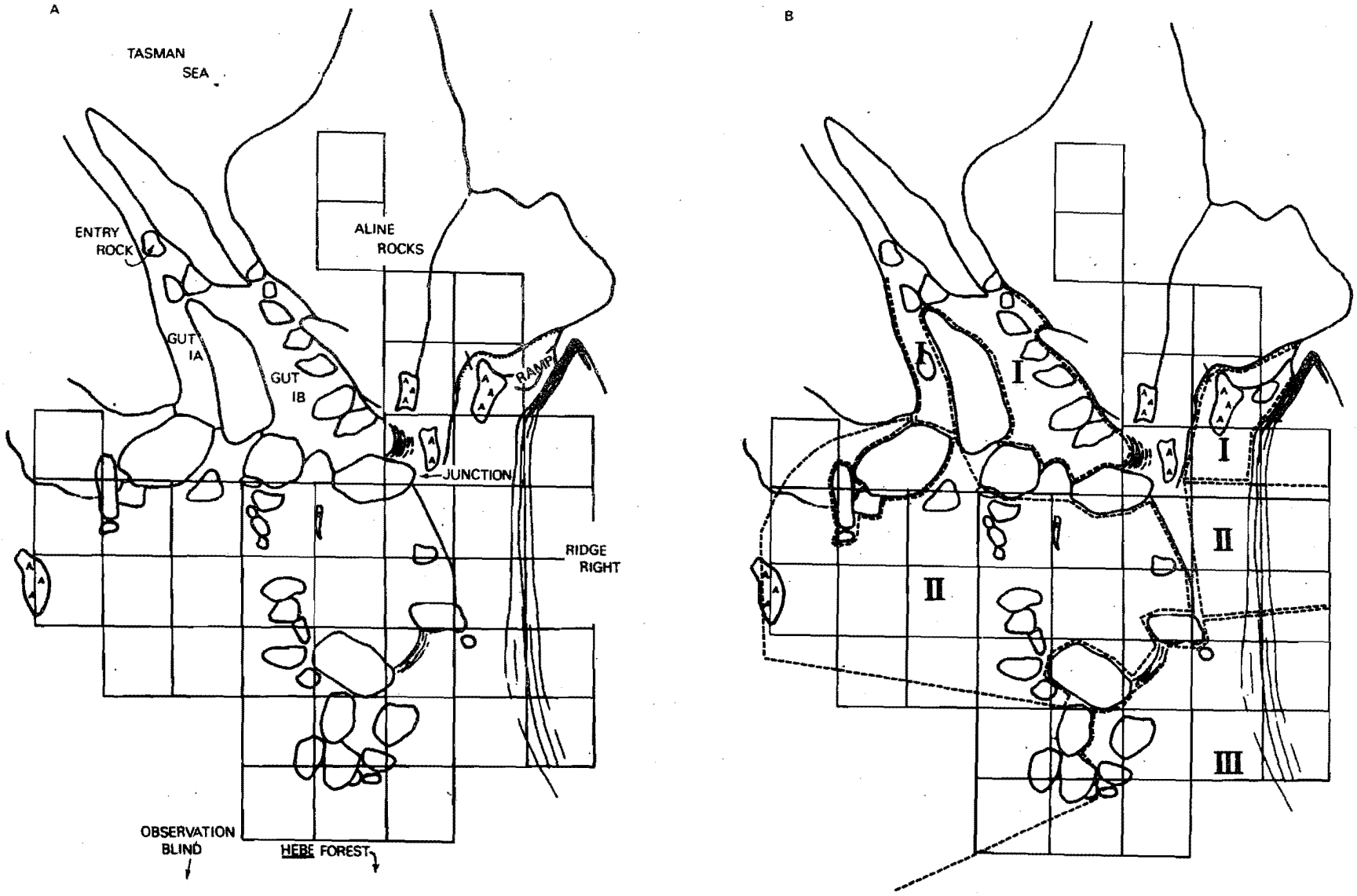

A
TASMAN
SEA
ENTRY
ROCK
ALINE
ROCKS
GUT
IA
GUT
IB
RAMP
JUNCTION
RIDGE
RIGHT
OBSERVATION
BLIND
HEBE FOREST
B
I
II
III

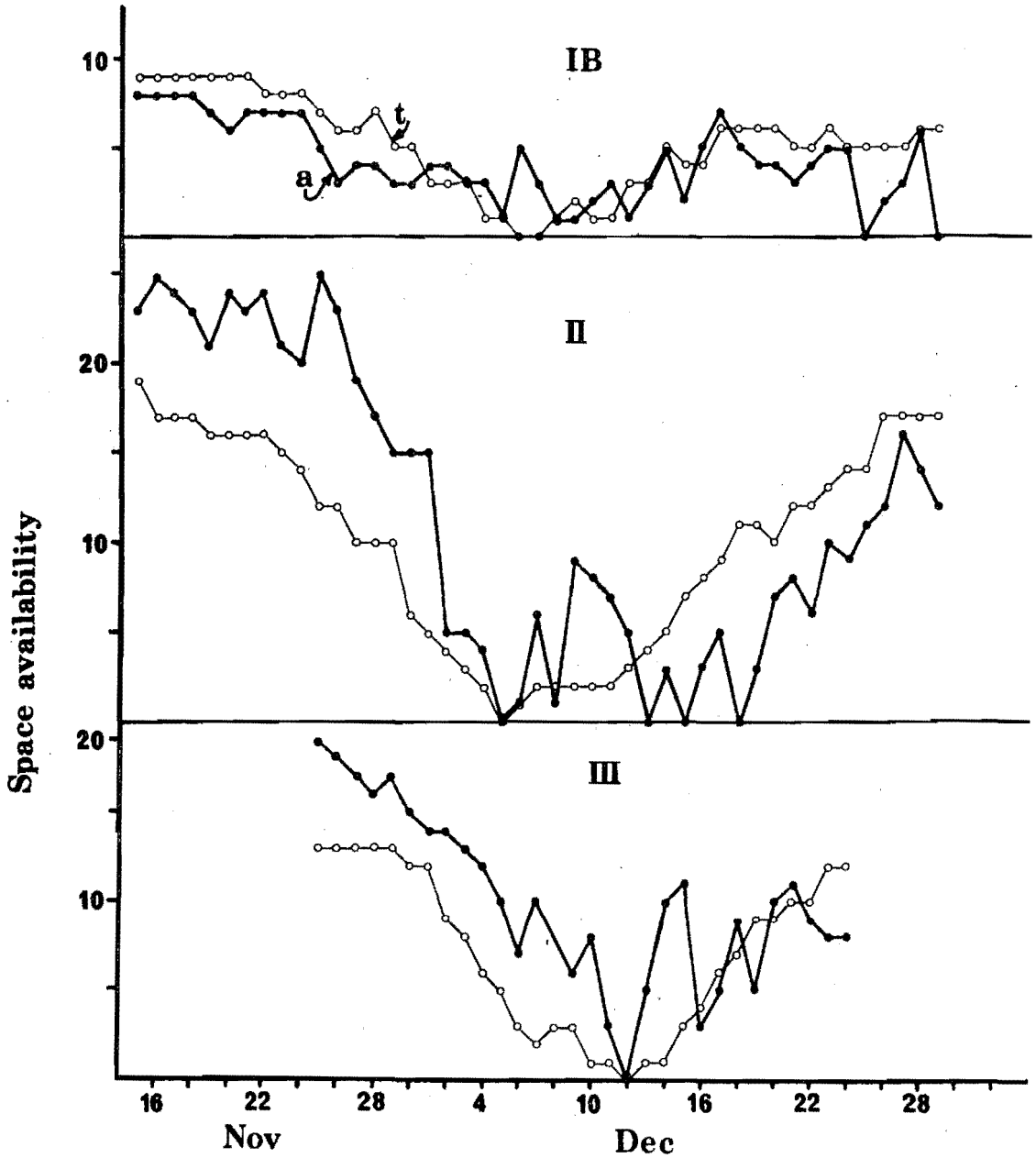
Figure 9. An analogous calculation can be performed for the observed data. The curve termed 'actual availability curve' in Figure 9 was plotted for the data points derived from the calculation ((seasonal maximum female census) - (observed female census)) for each day.

For Gut IB the theoretical and actual availability curves are similar, suggesting that the gut area was used intensively for breeding. The inland regions II and III show greater actual space availability than predicted, indicating that the areas reached saturation levels later than did IB, and that competition did not initially occur. After 13 December, the female population in region II was greater than predicted, and not until 17 December did region III show similarity in the curves.

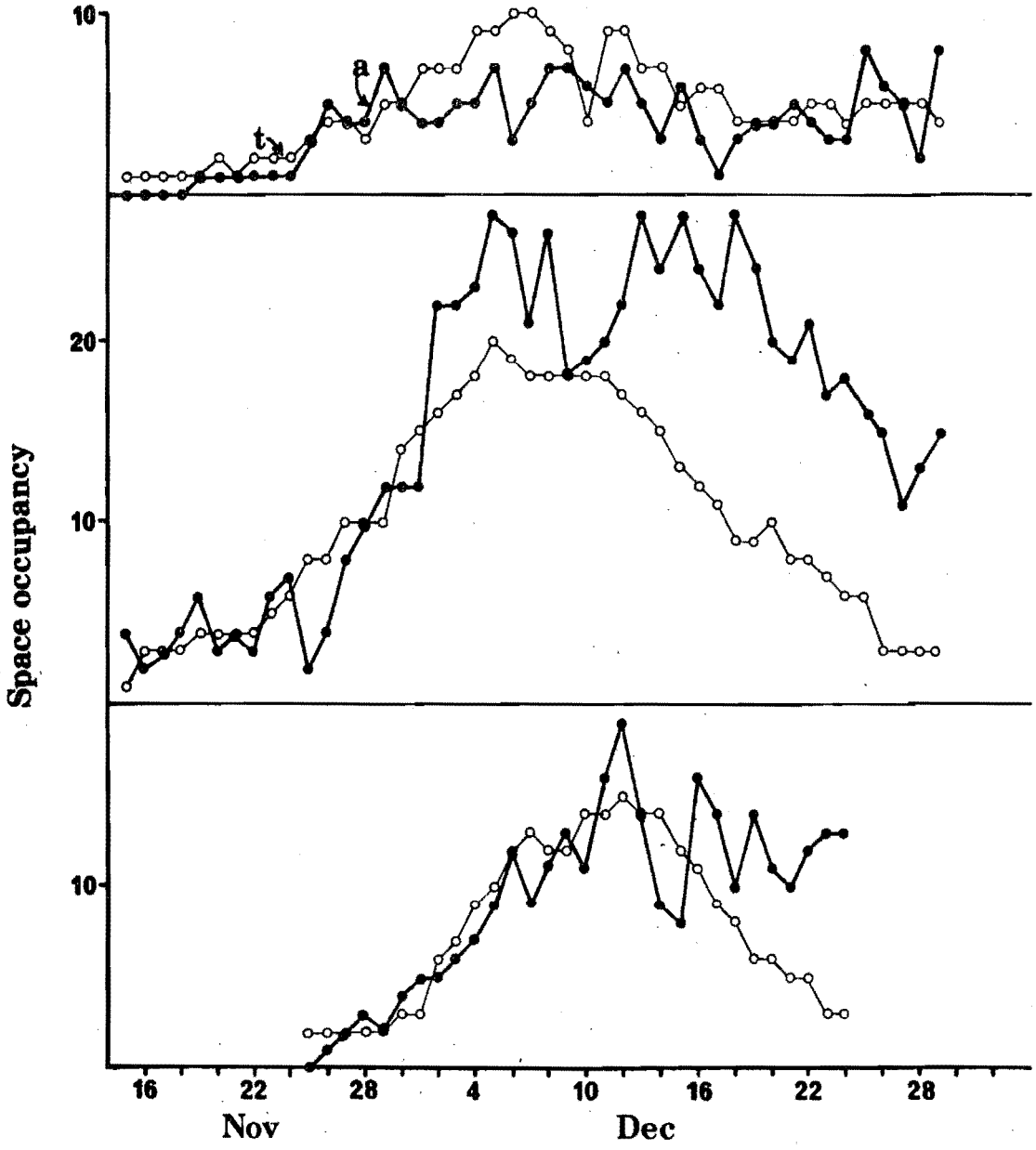
In summary, the theoretical space availability curve was a good predictor of the female census in gut IB, but for inland regions II and III it consistently underestimated the actual space availability for the first parts of the sample periods.

Another way of examining the same data is to assume that only those females who are in a 13-day peri-parturient period are in a birth region, and to compare the figures so obtained with the female census figures. The curves for these measures are plotted in Figure 10. The means for each pair of curves were compared by Student's t- or adjusted t-test for unequal variances. The results are: region IB, $t'_s = 2.23$, $0.02 < P < 0.05$; region II, $t_s = 3.45$, $0.001 < P < 0.01$; region III, $t_s = 1.11$, n.s. Thus in IB the actual number of females present was significantly smaller than the predicted number; for region II, female census figures were in excess of the predicted figures; and in region III, the theoretical and observed means were indistinguishable. These results suggest that

9. Seasonal distribution of actual (a) and theoretical (t) space availability for areas II, III, and Gut IB on the main study area.


IB
II
III
t
a
10
20
10
20
10
Space availability
16
22
28
4
10
16
22
28
Nov
Dec

10. Seasonal distribution of actual (a) and theoretical (t) space occupancy curves for the regions indicated in Figure 9.


Space occupancy
10
20
10
10
a
t
16
22
28
4
10
16
22
28
Nov
Dec

competition for space in IB curtailed the 13-day peri-parturient period, that the maximum number of females in region II was an unreliable estimate of saturation conditions, and that the number of females using region III can be accounted for solely in terms of the number of females who pupped there. Regions IB and II were favoured, but only IB was saturated.

2b. Competition for space; evidence from birth-dates. If some areas are favoured for pupping they should show a greater dispersion of pupping dates than other areas, because of continual replacement (or ousting) of females. If some regions become saturated, and remain so with the same individuals, the mean dates of pupping there could differ from those for less favoured areas, but the absence of differences between means does not necessarily mean that no preference is being shown. The relevant data are summarized in Tables 4 and 5. The inland region (III) of the main study area showed a significantly smaller variance of dates of birth than regions I and II. No significant differences between the means of birth dates within or between study areas were detected (for regions II vs III, $t'_{0.05} = 2.06$, $t'_s = 0.28$; for I vs III, $t'_{0.05} = 3.30$, $t'_s = 0.28$; for main vs subsidiary, $t_s = 1.23$, $P > 0.2$).

The region of the main study area which was farthest from the sea had significantly less dispersion of birth dates than did areas closer to shore, but no differences in mean birth dates were measured. It was suggested in the preceding section that IB became saturated, but II, because of the lack of agreement between actual and theoretical space availability curves and female census curves (Figures 9, 10) was not. If region III was used by females only because the other areas had many females present in them, this is evidence for avoidance of relatively crowded con-

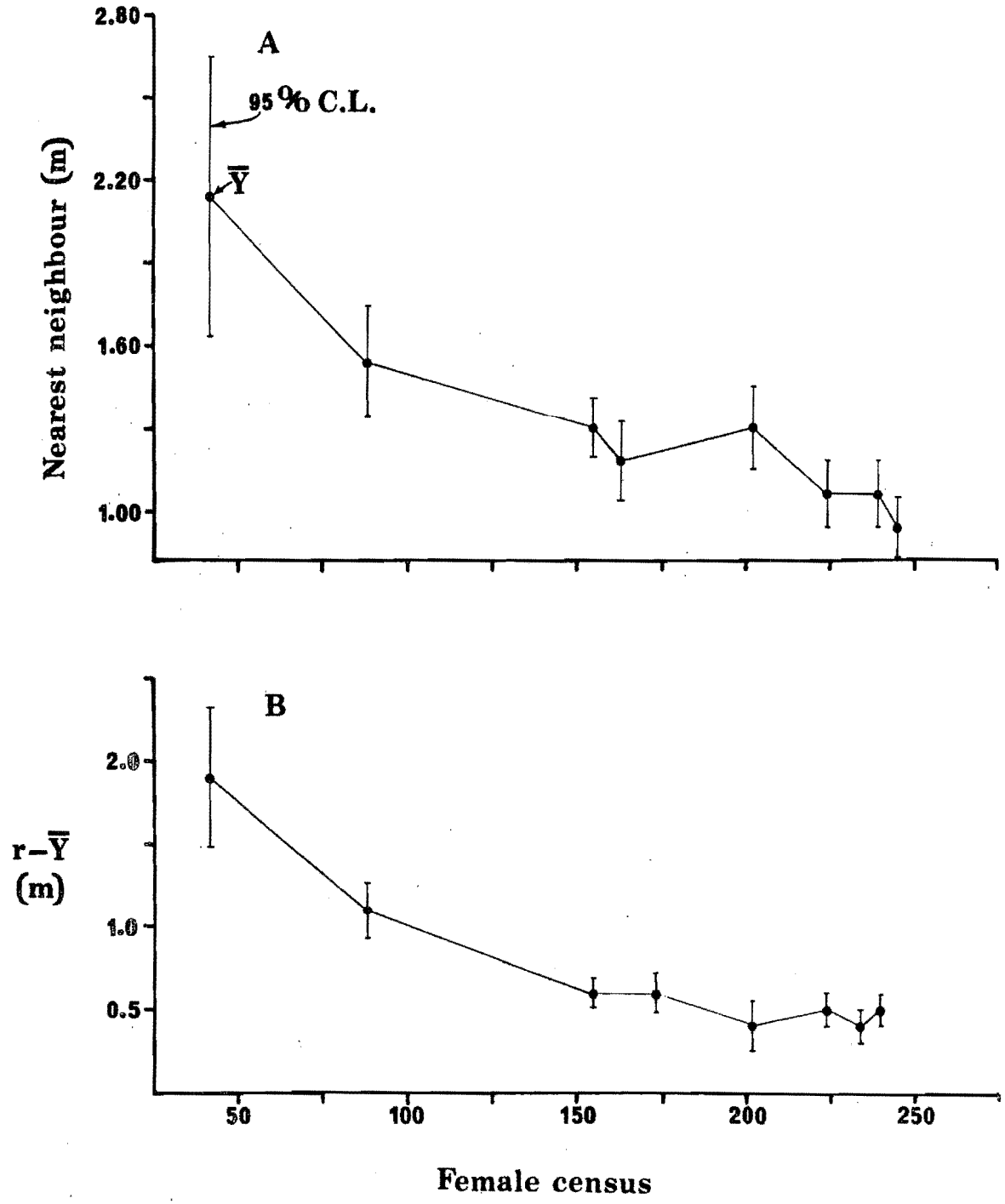
ditions by some pregnant females, even though crowding was not extreme. Crowding in regions II and IB did not prevent females from being recruited there, as indicated by the large dispersion of birth dates, and also, for region II, by the lack of agreement between the curves in Figure 10.

2c. Discussion: birth-dates and space-use by females. Dates of pupping vary systematically and regionally within single colonies of various species of pinnipeds. For example, in his study on Eumetopias, Gentry (1970: 53) observed that births occurred on one part of the island 17 days before the first birth on his study area. Hewer and Backhouse (1960: 171) noted that early calving in Halichoerus occurred on only a few available beaches, all of which eventually held pups. Working with the same species on the Farne Islands, Coulson and Hickling (1964: 497) noted that there was differential building up of the calf population on the islands in a similar pattern each year. Also for Halichoerus, differences in dates of calving have been noted on North Rona for 2 consecutive years, with one area being 1 to 2 weeks earlier than the other areas (Boyd and Laws, 1962: 255; Boyd, Lockie, and Hewer, 1962: 265).

2d. Competition for space: evidence from interindividual distances. In Figure 11A the means and 95% confidence limits for inter-female nearest neighbour distances are plotted against the number of females censused in each day-block. Only females less than 3.5m from their neighbours are included; others were considered as 'alone'. A general negative correlation exists between nearest-neighbour distance and female population. This was not a necessary

11. A. Relationship between inter-female nearest-neighbour distances and female censuses (per day-block).

B. Relationship between deviation from perfect over-dispersion and female censuses (per day-block). See text for explanation.


A
95% C.L.
$\bar{Y}$
Nearest neighbour (m)
2.80
2.20
1.60
1.00
B
$r-\bar{Y}$
(m)
2.0
1.0
0.5
50
100
150
200
250
Female census

accompaniment of increased population, because large areas of the study area were uninhabited (Figures 13, 15). In other words, females tolerated the closer proximity of neighbours not because they could not be avoided, but because preference for certain locations over-rode any repelling effect of decreased inter-individual distance.

Figure 12 summarizes the data on seasonal changes in the incidence of nearest-neighbour distance classes, for females. As the number of females on shore rose, the incidence of distance classes less than 2.0m increased, while the incidence of distance classes beyond 3.0m decreased.

The extent to which clumping of females occurs can be shown by comparing the measured mean nearest-neighbour distances with theoretical inter-female distances at perfect overdispersion. Females were sampled for nearest-neighbour distances over an area of approximately $440m^2$. The inter-individual distance at perfect overdispersion can be calculated as:

$$r = \sqrt{A' / 2\pi}$$

where r = inter-individual distance

A'= area theoretically 'available' to each female = (440/female census)

The relationship between deviation from perfect overdispersion, and the numbers of females ashore is shown in Figure 11B and Table 6. A general decrease in the deviation from perfect overdispersion was noted as the number of females on shore increased. Unlike Figure 11A, the confidence limits for day-blocks 5 and 6 do not overlap with one another or with those for day-blocks 7-12. In other words, the greater the number of females ashore,

TABLE 6:

RELATIONSHIP BETWEEN FEMALE CENSUS AND DEVIATION FROM PERFECT OVERDISPERSION

Day Block	Total Female Censuses[1]	r[2]	$\bar{Y}$[3]	$(r-\bar{Y})$	A'[4]
5	42	4.1	2.2	1.9	52.38
6	88	2.8	1.7	1.1	25.00
7	155	2.1	1.5	0.6	14.19
8	224	1.8	1.3	0.5	9.82
9	234	1.7	1.3	0.4	9.40
10	240	1.7	1.2	0.5	9.17
11	202	1.9	1.5	0.4	10.89
12	173	2.0	1.4	0.6	12.72

[1] Early morning censuses only.

[2] Theoretical maximum inter-female distance (metres), $r = \sqrt{(A/F)/\pi}$

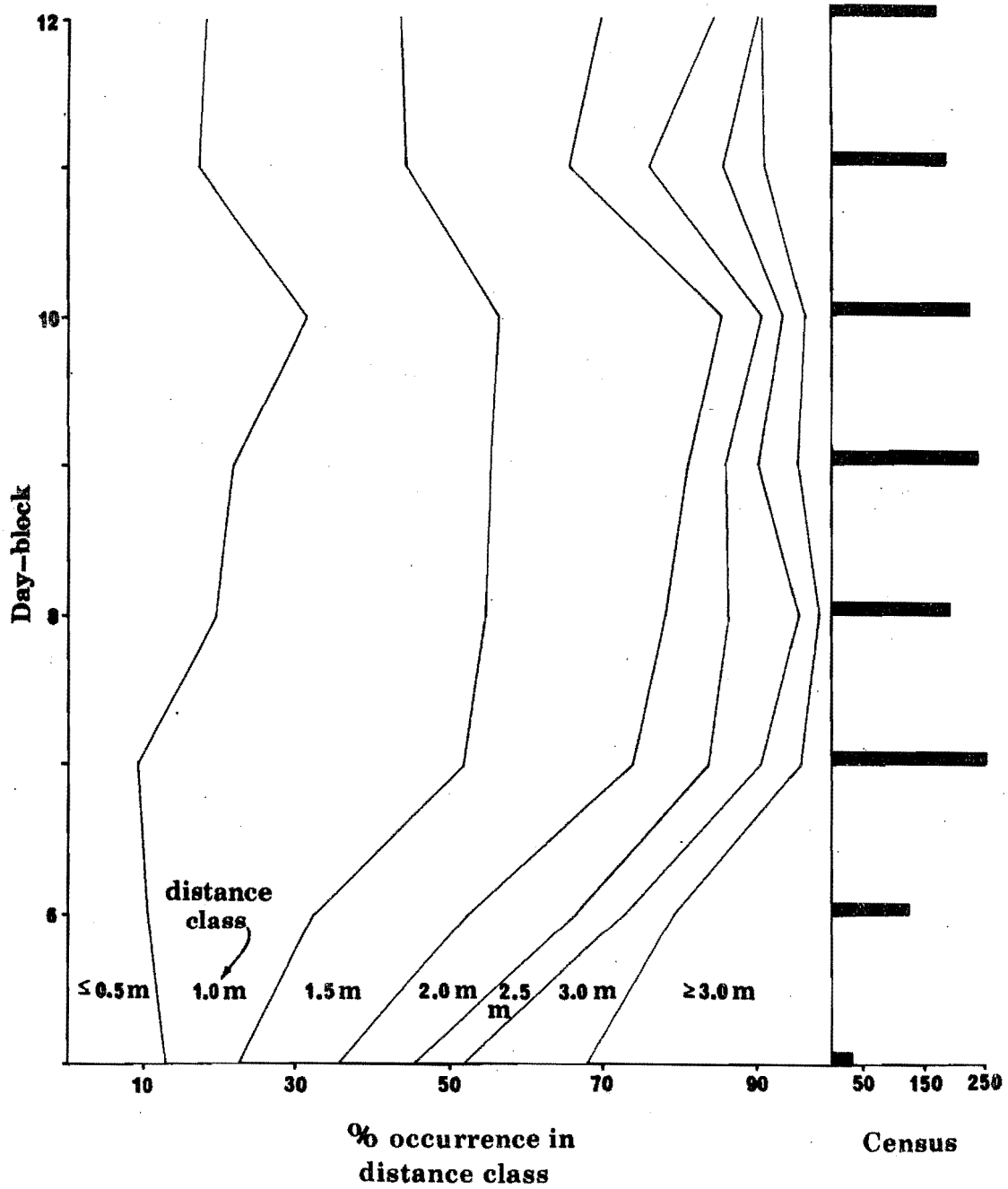
$= \sqrt{A'/\pi}$

where A = 440 square metres,
F = female census (per day)
π = 3.14159

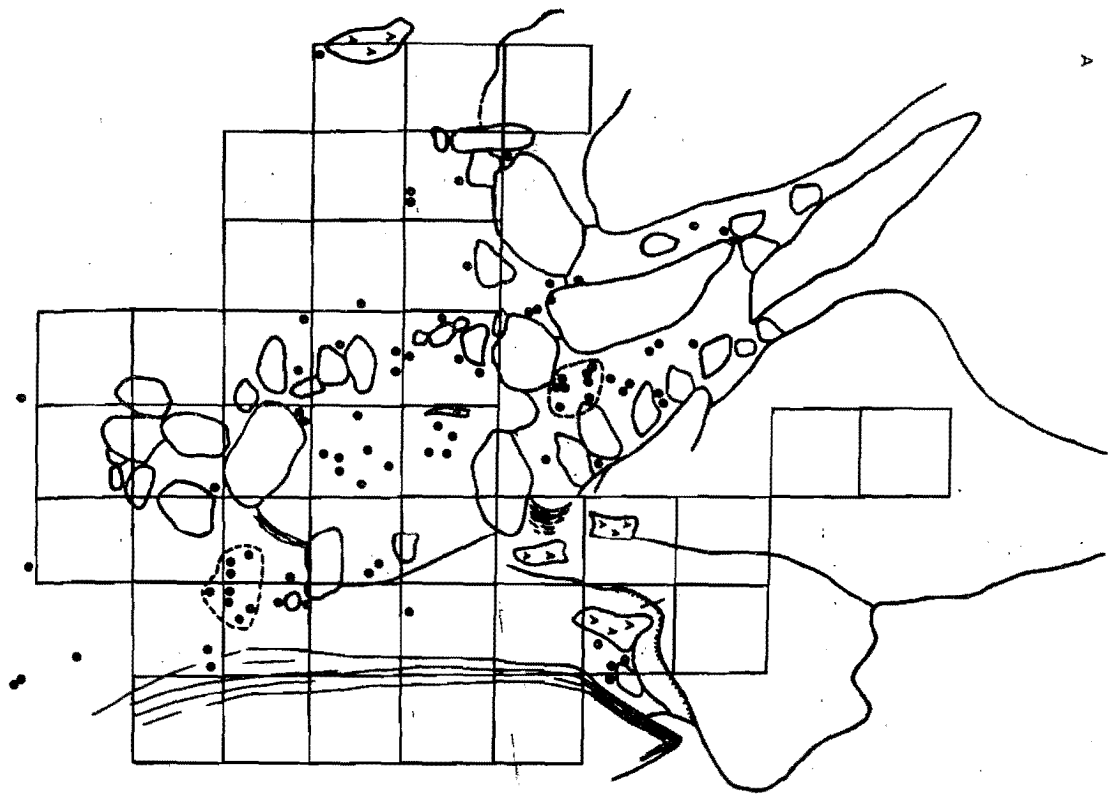
[3] Mean interindividual distance (metres)

[4] Area "available" to each female = $(440/F)$ (metres^2)

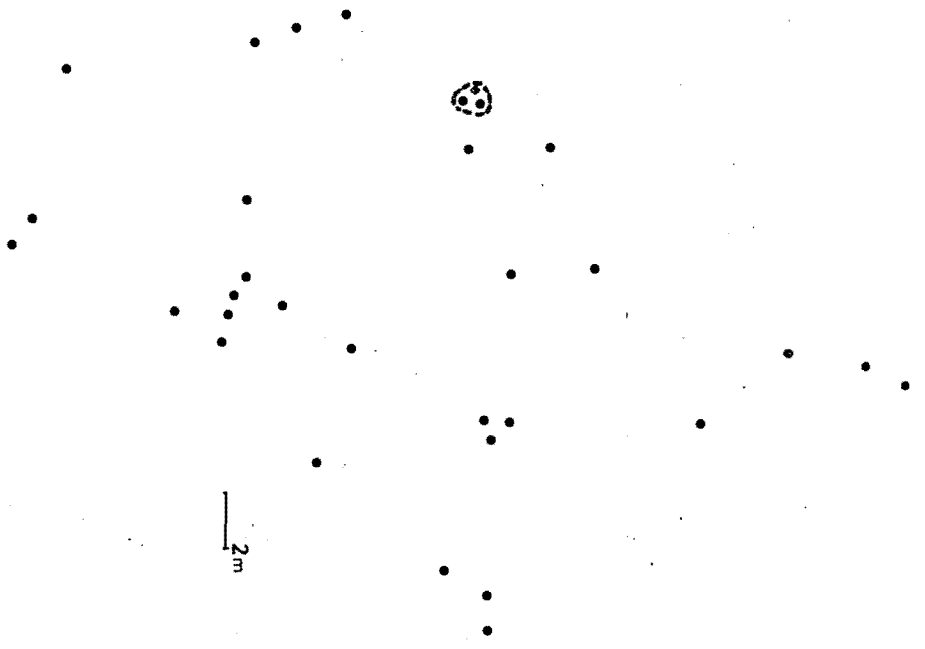
12. Seasonal trends in the percentages of females in different distance classes from their nearest female neighbours.


12
10
8
6
Day-block
distance class
≤0.5m
1.0m
1.5m
2.0m
2.5 m
3.0m
≥3.0m
10
30
50
70
90
50
150
250
% occurrence in distance class
Census

13. A, B. Dispersion of births on the main (A) and subsidiary (B) study areas.



A



B

the more closely was a perfectly overdispersed state approached. However, after about 30 females per day were ashore, no closer approach was achieved. This suggests that females localized at certain regions, avoided the crowded regions, and showed no tendency to fill in the unoccupied, little- preferred areas.

The irregular nature of the topography of the study area reduced distances over which animals could see unimpeded. Because of this, I tested whether such irregularities permitted greater concentrations of females to build up, than would build on featureless terrain, assuming that minimum nearest-neighbour distances are set by behavioural avoidance. The three nearest neighbours to each female were categorized as 'in sight' or 'out of sight' of the female in question, as judged by that female's ability to see the neighbours from the posture she was in, if she moved her head in any direction, including off the ground. Hence, females 'in sight' included females lying directly behind a female.

Females who were out of sight were in the minority (9.6%) and were at significantly greater distances than females in sight ($t'_s = 11.58$, $p < 0.001$) (Table 7). It is concluded that the nature of the terrain was not a factor in permitting dense aggregations of females to build up. The opposite is true, namely, that rough terrain forces increased inter-individual distances upon females. Reference to Plates 3A and 3B makes this clear. In these plates, males are separated by distances determined in large part by the presence of suitable rest ledges, between which no suitable locations exist. Animals must either be separated by at least the distance between ledges, or lie in contact with one another.

The data in Table 8 indicate that females have

TABLE 7:

NEAREST-3-FEMALE-NEIGHBOUR DISTANCES,
FOR "IN SIGHT" AND " OUT OF SIGHT" SITUATIONS

	$\bar{Y}$ [1]	S.E.	N	%
IN SIGHT	1.88	0.020	2380	90.4
OUT OF SIGHT	2.68	0.066	254	9.6

[1]Mean interindividual distance (metres) from nearest 3 females (only females less than 3.5 metres away are included).

TABLE 8:

COMPARISON OF NEAREST-FEMALE-NEIGHBOUR AND
NEAREST-3-FEMALE-NEIGHBOURS DISTANCES.

	$\bar{Y}$ [1]	S.E.	N
NEAREST-FEMALE-NEIGHBOUR	1.41	0.022	1381
NEAREST-3-FEMALE NEIGHBOURS	1.96	0.019	2634

[1]Mean inter-female distance (metres) (only females less than 3.5 metres away are included).

larger mean inter-individual distances when more than one neighbour is considered, than when only the nearest female is considered ($t'_s = 18.87$, $p < 0.001$). Therefore, the dispersion patterns of females can not be characterized only by nearest neighbour distances, since females show different inter-individual distances depending on the number of neighbours.

The relationship between interaction frequency, and the size of the female population, will be considered in Chapter IV C3b.

The evidence presented in this section strongly suggests that the density of females present on the breeding rocks on the Open Bay Islands is influenced directly by preferred habitat, distance from shoreline, and the density of females within female aggregations already present. The turnover of individual females in a region effects the same end as the presence of a high density of females. The data regarding the absolute numbers of females in gut IB indicate that the periparturient female population may shift in favour of incoming females, but behavioural data regarding dominance relations between females of these two classes are needed to substantiate this interpretation.

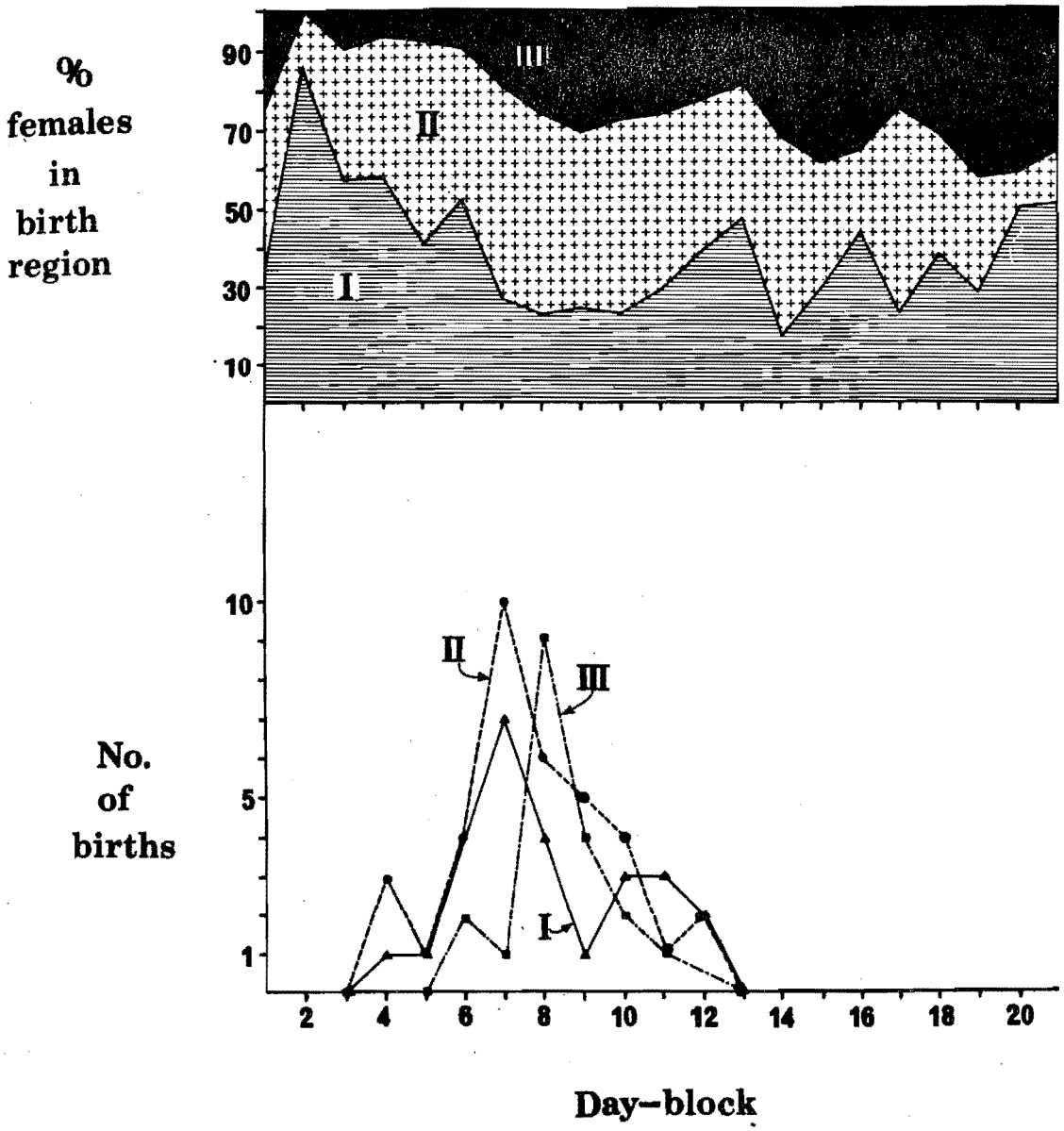
2e. Spatial distribution of births: Main and Subsidiary study areas. Figure 13 shows the distribution of births on the 2 study areas. The distribution shown for the main study area is probably complete, but that for parts of the subsidiary study area is not. It was impossible, without nearly continuous observation, to note the occurrence of all births, and relatively little observation time was spent at the subsidiary study area. The distribution of births on the clearly visible flat upper levels of the

subsidiary area is accurately portrayed; the sedentariness of recently parturient females, and the blood and placenta associated with birth, facilitated accurate assessment of the occurrence of births.

For both study areas, it is apparent that births did not occur regularly over the space available. For the main study area, clumping occurred in gut IB, in the central part of region II, and in part of region III. There were many areas which appeared suitable for pupping, but were almost unused (e.g. the left side of region III). Few births occurred on the featureless terrain on both study areas, and hillsides and the sides of knolls were avoided. Most births took place near some sort of topographical irregularity, such as a boulder, the side of a small cliff, or washed-up logs. Certain areas were preferred for pupping, and were used by a succession of females (Figure 13). This was obvious even in day-to-day observations, in seeing females give birth on almost exactly the same piece of ground as females before them. Minor movements away from such birthplaces did not appear to result directly from competition, but it may have operated on a subtle level. The same preferential use of locations for giving birth has been observed in Eumetopias (Sandegren, 1970: 34). Competition for space may occur for regions near the exact spot of birth, since, although females are sedentary, they do shift in position slightly after birth (see Chapter VB).

2f. Seasonal changes in female distribution: main study area. The seasonal trends in the numbers of females using different regions of the main study area are summarized in Figure 10. In Figure 14 the proportions of females using those regions are summarized with relation to dates

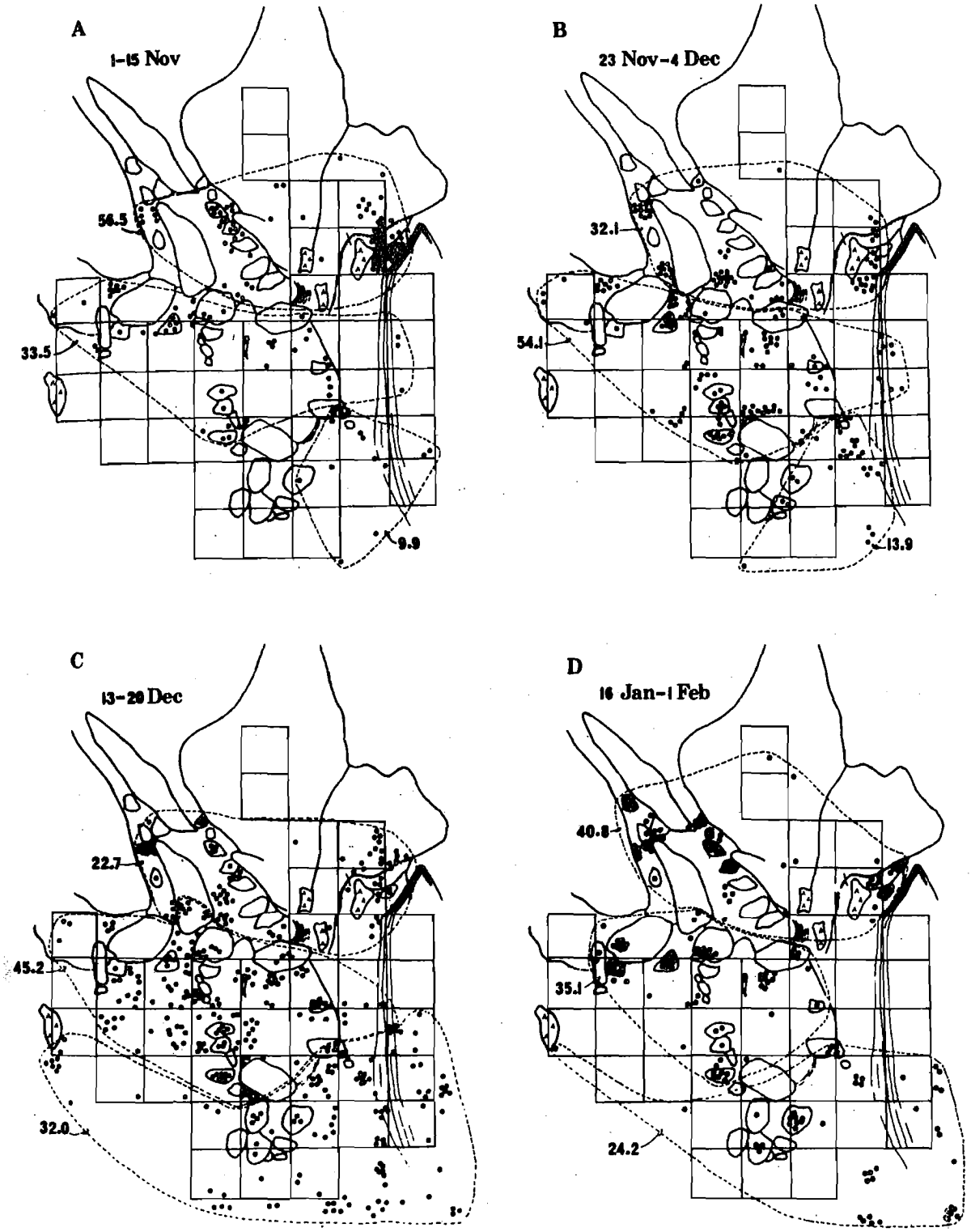
14. Seasonal trends in the percentages of females recorded within different birth regions (upper), and the numbers of births occurring on those areas (lower).


%
females
in
birth
region
90
70
50
30
10
III
II
I
10
5
1
II
III
I
No.
of
births
2
4
6
8
10
12
14
16
18
20
Day–block

of birth. Region I had the greatest proportion of females in the early phases of the summer, but region II held a slowly increasing proportion. Region III held the lowest fraction until day-block 6, and increased thereafter. By reference to Figure 11 it is seen that gut IB reached a peak level of females prior to the other regions (about 30 November), and region II peaked about a week before region III (6 and 13 December respectively). The trends in Figure 14 are in agreement with those in Figure 10, in showing how there was initially a high percentage of females in region I, which decreased as regions II and III were sequentially built up. A number of important trends are obscured by such treatment, Changes in the distribution of females on land throughout the summer are summarized in Figure 15. Most of the females were concentrated in shoreline regions during early November, particularly near the Ramp region (Figure 15A). By late November to early December (Figure 15B) many more females were recorded on the upper levels, the guts still harboured fairly constant numbers of females, but many fewer females were recorded on the Ramp. This pattern was essentially unchanged in mid-December (Figure 15C), but by the last half of January the dispersion of females had begun to resemble that seen in early summer (Figure 15D).

It is difficult to separate the effects of season and temperature. Both early and late summer were warm and dry. During the observation period in late May - early June 1971, many animals were on the upper levels and in the woods (see below), and the weather was cool and overcast.

15. A-D. Seasonal changes in dispersion patterns of females. The figures refer to the percentages of females recorded in the areas indicated.


A
1–15 Nov
56.5
33.5
9.9
B
23 Nov–4 Dec
32.1
54.1
13.9
C
13–28 Dec
22.7
45.2
32.0
D
16 Jan–1 Feb
40.8
35.1
24.2

2g. Discussion: Summer dispersion patterns on the Open Bay Islands. The early concentration of females in region I occurred too early in the summer, when few females were present, to be a manifestation of competition for space among pregnant and parturient females. Also, the distribution at that time was heavily in favour of a location (the Ramp) which was subsequently used very little for pupping. It is concluded that the trends observed for population changes in gut IB and regions II and III reflect competition for space in IB, and preferential avoidance of certain areas. Females without pups tended to localize in regions of very easy access to the sea (Figure 15A) in early summer, but most females with pups concentrated on areas which were the same as those used intensively for pupping. Gut IB was probably the only region on the main study area which was, in social terms, 'saturated', and many areas were not used at all.

The extent to which philopatry (Mayr, 1963: 568) affects an individual's behaviour in attempting to claim a particular location for pupping is not known. Peterson (1965: 121-122) observed marked site tenacity in seven female Callorhinus, who pupped within metres of the same locations for 3 years consecutively; R. W. Rand (1967 : 19) noted 'claims' by individual adult female A. p. pusillus for particular rest locations to persist more than a year; and Cameron (1971) noted resting site fidelity in Halichoerus females to last up to a few years.

The role which herding plays in affecting the distribution and dispersion of female A. forsteri is unknown, but it does not serve to simply contain females within territories (Chapter III A8a). In contrast, Peterson (1965: 121) stated that 'females probably can

not reach the locations of their choice... because of the possessiveness of the bulls', implying that Callorhinus bulls are capable of altering the space-use patterns of females. If this is true, then there must be some regularity in how bulls herd in certain regions, or how females respond to herding, to engender the site tenacity he observed in females. Some individual females on the Open Bay Islands showed strong inclinations to localize in their movements, and to use particular rocks and ledges for resting, but the role of such preferences in affecting female dispersion is not known. Darling and Boyd (1969: 296-297) suggested that pregnant Halichoerus cows may choose one of a few adjacent islands on which to bear young depending on how the immediate weather conditions affect accessibility to the island. The same authors mentioned that the presence of humans can induce cows to move elsewhere to calve (ibid.). In their study of Halichoerus on the Farne Islands, Coulson and Hickling (1964: 495) concluded that 'initial selection of a breeding island is conditioned by the state of the sea, and later breeders are attracted to the area already occupied by breeding cows'. So well-documented is fidelity to home rookeries by fur seals, it seems unlikely that similar behavioural plasticity prevails to the same extent as for Halichoerus.

Differences in dates of calving between shoreline locations and inland locations were documented by Coulson and Hickling (1964: 498) for Halichoerus; their conclusions were similar to mine, namely, that shoreline is a preferred calving zone, but the avoidance of crowded conditions induces females to move inland. As indicated earlier, differences in mean dates of pupping may or may not accompany an 'overflowing' of females into underpopulated zones,

but a wide spread of birth dates, if coincident with a consistently high density of breeding animals, should be indicative of a favoured pupping area.

It can be concluded that topography, and the presence of females, affected the spatial distribution of births, and that the presence of females affected the temporal distribution of births. During the period when, theoretically, the largest numbers of oestrous females were present (see Chapter III), the dispersion of females on the main study area was affected by topography and other females. Whatever factors are responsible for engendering the observed patterns of pre-and post-breeding distribution of females, they do not appear to modify distribution in the breeding period. Females with young pups seemed to be more aggressive than females with older pups, and the proportion of recent mothers may affect the mean inter-individual distance, and thus affect density within concentrations of females, but no data were gathered on this matter.

The possible role of females being attracted to already-existing concentrations of females in affecting dispersion and distribution is difficult to assess, and was compounded by habitat preferences. Although the magnitudes of the two are in doubt, both habitat preference and competition for space are partial determinants of the observed pattern of space use by females.

2h. Winter dispersion patterns: general. During the summer, few females hauled out in the forest, although on hot days it was used extensively in places. As pups matured they used regular paths through the forest between the main and the subsidiary study areas. There were a few SAMs scattered throughout the forest behind the breeding rocks.

In May and June 1971, the numbers of individuals in different sex and age classes using the breeding rocks and the woods were counted (Table 9). Small males were greatly in the majority among the male population ashore, and the proportions of males in the forest varied inversely with their size class. No comparable figures are available for the summer distribution by habitat type, but there seemed to be many more pups in the forest during the winter observations (101/299 = 33.8%) than during the summer.

2i. Possible historical changes in habitat use on the Open Bay Islands. The history of fur seals on the Open Bay Islands is almost unknown, but it is definite that many more existed there in the early 1800's than at present. A team of men marooned on the Open Bay Islands in 1810 collected over 11,000 skins in less than a year (May,1967: 25). However, Burrows (in press) has suggested that the islands used to have a more open vegetation, so the much larger population present in the early 1800's may have been less restricted than the present population in breeding distribution on the island. Knowing the habitat preference of the seals, however, it is likely that with greater numbers the breeding density was increased.

TABLE 9:

HABITAT PREFERENCES OF DIFFERENT CLASSES,
OPEN BAY ISLANDS, MAY - JUNE 1971

CLASS	ON BREEDING ROCKS	IN FOREST	TOTAL
ADULT MALES	6	0	6
LARGE SAMS	20	0	20
MEDIUM-LARGE SAMS	32	2	34
MEDIUM/SMALL SAMS	38	15	53
FEMALES	156	17	173
PUPS	198	101	299
PUPS: Lone (%) *	103 (50.5)	59 (63.4)	162
PUPS: Groups (%)	53 (25.9)	30 (32.3)	83
PUPS: With females (%)	48 (23.5)	4 (4.3)	52

* % of pups in association indicated, in habitat type.